Variation in alloparental care in dwarf mongooses

Emily Grout

September 2019

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master of Science in the Faculty of Life Sciences.

Word count: 15237 (excluding references)

Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Abstract

Alloparental care (the provision of care to offspring by adults other than the parents) is widespread in social vertebrates. However, there is much unexplained variation in the contributions of different group members to these helping activities. Dwarf mongooses (*Helogale parvula*) live in groups of 5 to 30 individuals, consisting of a dominant breeding pair and subordinate adult helpers of both sexes. All adults contribute to feeding, grooming and group-sleeping with the young. I used detailed observations from seven wild but habituated dwarf mongoose groups to examine whether sex, dominance status and age influence variation in alloparental care. I found that subordinates, especially younger individuals, fed pups more frequently than dominants, but dominants brought larger prey items than subordinates. Subordinate females groomed pups more frequently than dominant females, but there was no difference in grooming frequency between dominant and subordinate males. Additionally, subordinates groomed pups for longer durations than dominants. I found no evidence that male or female helpers preferentially feed or groom pups of a particular sex. Furthermore, there was no significant difference between helpers in group-sleeping bouts. To test whether adults preferentially feed certain pups, a playback experiment using pup begging calls was designed, and pilot trials conducted. Preliminary results indicated that neither sex nor age of subordinate group members influenced their mean response latency to respond to different begging tracks, but a full experiment would be needed for strong conclusions. In summary, I found that there is variation between group members in their level of investment in different alloparental tasks. Therefore, future studies on variation in alloparental behaviour should consider multiple caring activities exhibited by group members to obtain a broader understanding of the factors involved, and to extend our understanding of cooperation, parental care and social living.

Acknowledgements

Firstly, I would like to thank my supervisor Professor Andy Radford who has given me the opportunity to conduct this study as well as supporting me throughout the project. I would like to thank O. Niedzialek, D. Lagan, K. Hollingworth who assisted with the data collection in the field, without which I would not have had access to such a rich data set in a short time period. I am sincerely grateful for A. Morris-Drake and Dr Laura Richardson who have given support throughout the project, particularly with modelling using RStudio. I would also like to thank Lydia Dashley Giddings and Ines Goncalves for reading my thesis and giving helpful corrections. Thank you to B. Rouwhorst and H. Yeates for access to their land. Finally, I would like to thank my friends and family who have given encouragement throughout the project.

Contents

List of Tables

List of Figures

Chapter 1: General Introduction

1.1 Cooperative Breeding

Cooperative breeding is a social system where adults other that the breeding pair help to raise offspring. It is found in a variety of taxa (Koenig & Dickinson 2016) including mammals (Macdonald & Moehlman 1982; Jennions & Macdonald 1994; Solomon & French 1997), fish (Wisenden 1999), birds (Stacey & Koenig 1990; Emlen & Vehrencamp 1983) and insects (Klepzig & Taborsky 2011). A 'helper' was defined by Brown (1987) as "an individual that performs parent-like behaviour toward young that are not genetically its own offspring… Helpers may be altruistic, cooperative, or selfish. Note that breeding status and conferral of benefit or harm to recipient or helper are irrelevant to the definition".

Social groups vary in their level of cooperation. Clutton-Brock (2006) has defined four types of cooperative breeding: group breeders, communal breeders, facultative cooperative breeders and obligate cooperative breeders. Group breeding is where multiple breeding females in one group synchronise their births. Species which exhibit this breeding strategy include locusts (*Locusta migratoria*) (He *et al*. 2016), many ungulates (Jarman 1974), many bats (O'Donnell 2002) and white-nosed coatis (*Nasua narica*) (Beisiegel 2001). Communal breeding is where multiple females within the same group give birth and the offspring are raised by other breeding females as well as non-breeding females and males. Examples of species which exhibit this breeding strategy include spotted hyenas (*Crocuta crocuta*) (Gittleman 1989), banded mongooses (*Mungos mungo*) (Gilchrist *et al.* 2004) and evening bats (*Nycticeius humeralis*) (Wilkinson 1992). Facultative cooperative breeding is where offspring can be cared for by non-breeding males and females, although their help is not essential for raising the offspring. This breeding system is exhibited in red wolves (*Canis lupus rufus*) (Sparkman *et al*. 2010) and silver backed jackals (*Canis mesomelas*) (Moehlman 1979) as well as species in the marmoset and tamarin families (Callitrichidae) (Goldizen 1987). The final type of breeding strategy is obligate cooperative breeding. This is where the breeding pair cannot raise offspring without the help of other group members. The number of non-breeding adults within the group outnumbers the breeders and these helpers have a large role in the caring activities. Examples of species which exhibit this breeding strategy include pied babblers (*Turdoides bicolor)* (Nelson-Flower *et al*. 2011), the cichlid

Lamprologus brichardi (Taborsky & Limberger 1981), meerkats (*Suricata suricatta*) (Clutton-Brock *et al*. 2001), wild dogs (*Lycaon pictus*) (Creel *et al.* 1997), naked mole-rats (*Heterocephalus glaber*) (Jarvis 1981) and dwarf mongooses (*Helogale parvula*) (Courchamp *et al.* 1999).

One main reason why helpers might be present in a group is if offspring do not immediately disperse to breed independently. The decision to stay at home rather than disperse can be explained by ecological constraints and/or benefits of philopatry, which are not mutually exclusive (Nelson-Flower *et al.* 2018). Ecological constraints include lack of suitable territories and mates and high dispersal costs. For example, acorn woodpeckers (*Melanerpes formicivorus*) exhibit flexible breeding strategies depending on territory quality; individuals will remain in the natal territory if there is a shortage of unoccupied breeding territories (Stacey & Ligon 1987). Conversely Siberian jays (*Perisoreus infaustus*) however will stay in their natal territory if there are a lack of mates because they are more likely to gain future breeding opportunities by remaining (Kokko & Ekman 2002). Furthermore, individuals could stay at home because the cost of dispersal is too great, as found in naked mole-rats (Burda *et al*. 2000). In many species, gaining helping experience (philopatric benefits) before an individual reproduces will increase the quality of reproductive performance (Brown 1987; Korndeur 1996; Margulis 2005). Therefore, choosing to remain with the parents to assist with the rearing of subsequent litters could accrue long-term reproductive benefits. In mandarin voles (*Microtus mandarinus*), for example, males that have had previous experience with novel pups as well as with mating and paternal experience showed increased alloparental behaviours towards novel pups (Song 2010). Furthermore, a translocation experiment found that Seychelles warblers (*Acrocephalus sechellensis*) had higher lifetime reproductive success if they had previous helping experience (Korndeur 1996).

Helpers can also arise in other ways; for instance, unrelated individuals may emigrate to a new group and assist with rearing unrelated offspring. This is seen in dwarf mongooses (Rasa 1977; Rood 1983), meerkats (Clutton-Brock *et al.* 2000) and pied kingfishers (*Ceryle rudis*) (Reyer 1986). The presence of individuals in a group when offspring are born, whatever the initial reason for their presence, does not automatically elicit helping behaviour. There are three main explanations for helping behaviour in cooperatively breeding species —coercion, indirect fitness benefits and direct fitness benefits — which are not mutually exclusive (Bergmüller *et al*. 2007).

1.1.1 Coercion

Non-breeding group members may care for the offspring of breeders as a form of 'rent payment' to avoid eviction by the dominant individuals (Gaston 1978; Kokko *et al.* 2002). Evidence for 'paying rent' has been limited in the literature, with most work done on the cooperatively breeding cichlid *Neolamprologus pulcher* (Bergmüller & Taborsky 2005). If an adult has a greater benefit from living in the social group in the long term, the cost of helping another individual's offspring to remain in the group could be outweighed by potential future benefits such as acquisition of mates and resources. If helpers are not investing enough energy in cooperative acts, they could either be encouraged to help or are evicted from the group which would hinder their survival and reproductive success. Evidence of evictions have been convincingly found in fish (Ang & Manica 2010) as well as in a variety of mammals such as spotted hyenas (Holekamp *et al.* 1993), house mice (*Mus musculus*) (Gerlach 1996), black tufted-ear marmosets (*Callithrix penicillata*) (Schaffner & French 1997) and banded mongooses (Gilchrist 2006), although eviction is relatively uncommon when helpers reduce their contributions to cooperative acts (Clutton-Brock 2002). Furthermore, a study on naked mole-rats found that when the dominant female (who elicits punishment to 'lazy' workers) is removed, the helpers will continue to care for the young; their investment in caring activities may, however, be reduced (Reeve 1992).

1.1.2 Indirect benefits

The inclusive fitness theory has been the most well-recognised theory to explain the evolution of cooperative acts. The evolution of altruistic behaviours through high relatedness was initially stated by Haldane (1955) and later supported by Hamilton (1964), coining the term 'inclusive fitness' which mathematically explains the adaptive benefit of cooperative breeding. For cooperative care to occur, Hamilton described two assumptions which should be met: individuals must recognise kin and movement must be slow from place of birth. This theory has been supported by many studies (Hughes *et al*. 2008).

In social mammals, there is strong evidence that individuals can recognise others of close relation (Gompper *et al.* 1997; Holekamp *et al*. 1997; Gobush *et al*. 2009); this ability is also seen in fish (Gerlach & Lysiak 2006) and birds (Shields 1984; Beecher 1988; Leclaire *et al*. 2013). Previous research has found that cooperatively breeding mammals are able to identify relatives through various mechanisms including vocal cues (Hammerschmidt & Fischer 1998; Müller & Manser 2008) and phenotype matching (Leclaire *et al.* 2013). When resources are scarce, the benefits of kin discrimination are apparent in maintaining a social group rather than dispersing, because cooperative acts can benefit those highly related recipients (Griffin & West 2003; Cornwallis *et al.* 2009). However, in cooperatively breeding meerkats, adults do not vary their level of contribution to pup care between offspring of varying relatedness (Clutton-Brock *et al*. 2001). Moreover, in banded mongooses, pup sex is more important than relatedness for adults choosing which pups to escort (Vitikainen *et al*. 2017).

Inclusive fitness theory has been the most popular concept to explain the evolution of cooperative behaviour (Abbot *et al.* 2011). However, it does not explain cooperation between species (Sachs *et al*. 2004) as well as cooperation between unrelated individuals of the same species, with recent research suggesting that the importance of inclusive fitness theory has been overestimated (Griffin & West 2002). The evolution of cooperation between non-kin has sparked debate between scientists (Birch & Okasha 2015) with other theories being brought forward to attempt to explain these phenomena which include intra-specific mutualism, manipulation and reciprocal altruism (Clutton-Brock 2009), as well as environmental stochasticity (Kennedy *et al*. 2018).

1.1.3 Direct benefits

Living in a group can be advantageous for multiple reasons including collective defence, shared vigilance, reduced predation risk, increased foraging success, gain of parental experience, gaining reciprocally altruistic partners and increased grooming opportunities (Trivers 1971; Foster & Treherne 1981; Silk *et al*. 2003; Thünken *et al*. 2014; Jungwirth *et al.* 2015; Langergraber *et al*. 2017). Therefore, acting cooperatively may evolve if it leads to the increase in group size (Wiley & Rabenold 1984) and associated direct benefits (Silk *et al*. 2003; Cameron *et al*. 2009).

Communal defence against conspecific rivals is an indirect form of cooperative care which can have direct benefits to the helper. Defending the group's territory is vital for maintaining access to resources as well as the breeding success of particular group members (Radford 2003), therefore living in a group is beneficial for all group members, although the benefits from participating in intergroup conflict will vary between group members (Radford *et al*. 2016). Familiarity of opponents and the level of threat have been found to influence encounter intensity (Wich & Sterck 2007). Behaviours elicited from encounters between groups vary from 'neutral' interactions, where information between the groups are gathered, to fighting, which could result in serious injuries and death (Mosser & Packer 2009). Communal defence of a territory is now thought to be an important factor for driving group-living even in noncooperative species (Port *et al*. 2011). Work conducted on multi-male primate groups has found that communal defence from subordinate males increased total reproductive success of both dominant and subordinate males (Snyder-Mackler *et al.* 2012). Therefore, acting cooperatively in communal defence could benefit the helper because helpers will have access to resources and, as seen in primates, could potentially increase their own reproductive success as a result.

There are multiple anti-predator behaviours exhibited by different species (Lehtonen & Jaatinen 2016), such as increasing predator confusion (Foster & Treherne 1981), mobbing (Kern & Radford 2016), communal defence (Hass & Valenzuela 2002) and vigilance (Lima 1995). Living in groups can reduce individual investment in anti-predator behaviours (Brown & Brown 1987; Arroyo *et al*. 2001; Jungwirth *et al.* 2015), which is beneficial because they are often costly (Blumstein & Daniel 2005). For instance, in species that spend a large proportion of time foraging, it can be beneficial to have one individual monitoring predation risks and providing information to the others (Kern & Radford 2013). Sentinel behaviour, where an individual adopts a raised position to scan for danger, is seen across a wide variety of taxa from birds (Wright *et al.* 2001), mammals (Quenette 1990) and more recently found in fish (Brandl & Bellwood 2015). There are conflicting theories for the evolution of sentinel behaviour. It was originally believed to be a selfless act by the sentinel because they are trading foraging time to aid the survival of groupmates, and this has been supported by research conducted on wild pied babblers (Ridley *et al*. 2013). However, this behaviour can also be viewed as a selfish act because the sentinel will have a reduced risk of being preyed upon (Clutton-Brock *et al*. 1999) and could receive future

benefits from group members in other modalities such as grooming (Kern & Radford 2018). It was originally hypothesised that living in a larger group reduces an individual's vigilance (Lima 1995), which could cause the development of larger aggregations to increase each individual's foraging time. However, it has also be argued that reduced individual vigilance levels (from living in larger groups) could be caused by reduced predation threat per individual, suggesting the dilution effect is the cause for reduced vigilance (Roberts 1996). It is likely that the benefit of living in a large group is due to a combination of the benefits from collective defence, sharing vigilance and dilution effect (Lehtonen & Jaatinen 2016).

Group-living and being part of a larger group could lead to improved foraging success through information transfer when individuals have spatial memory of high-quality feeding sites (Evans *et al.* 2016; Falcón-Cortés *et al.* 2019). Moreover, in species that forage by disturbing the substrate, individuals could benefit by foraging in close proximity to others as prey which escape one individual could be caught by another group member (Kaufmann 1962). Experimental research on group-living in crab spiders (Thomisidae) found that groups were more likely to attack larger prey which could be shared between group members and that they had higher prey capture success compared to solitary individuals (Herberstein & Schneider 2018). In particular ecological conditions, the benefit of living in larger groups and hunting cooperatively has been found to increase food intake rate compared to solitary hunters (Clark & Mangel 1986); cooperative hunting can allow individuals to coordinate attack to capture challenging prey (Smith *et al.* 1981). Moreover, in white-nosed coatis, females that forage in groups are able to displace solitary males when food sources become patchy (Gompper 1996).

What was originally believed to be an act of altruism, cooperative care has also been suggested to be an indirect signal of quality of foraging success to other group members without being a dominant individual (Zahavi 1995). This honest signal of quality (also known as the 'handicap principle') could increase the helper's social status, and potentially increasing their future acquisition of mates and probability of gaining dominance status in the future (Wright 1999). However, there are currently a limited number of studies which have supported this theory (Zahavi 1990; Wright 1997); Freeman-Gallant (1996) found in savannah sparrows (*Passerculus sandwichensis*) that females were more likely

to choose mates which fed chicks at higher rates. However, there has been no evidence for cooperative care to be used as a signal of quality in cooperatively breeding species.

Grooming serves a variety of benefits which could cause group members to remain together and act cooperatively. Benefits of grooming range from removing ectoparasites and reducing stress levels to maintaining social bonds and increasing infant survival (Silk *et al*. 2003, 2009; Wittig *et al*. 2008; Russell & Phelps 2013). In wild horses (*Equus ferus*), grooming between unrelated individuals increases their reproductive success, which demonstrates the adaptive benefits of cooperative behaviour alone (Cameron *et al*. 2009). Furthermore, in common marmosets (*Callithrix jacchus)*, grooming has been hypothesised to be a form of service to gain coalitionary support; breeding females may use it as a form of payment to non-breeding females to remain in the group and assist with offspring caring activities (Lazaro-Perea *et al*. 2004). The use of grooming as a form of payment has also been observed in other species including chimpanzees (*Pan troglodytes*) and dwarf mongooses (Fedurek 2009; Kern & Radford 2018). As many group-living species exhibit grooming behaviours (which have been found to increase the likelihood of survival and reproductive success), individuals could be acting cooperatively to remain in the group to have access to such grooming opportunities.

1.2 Types of alloparental behaviour

In cooperatively breeding species, helpers can significantly influence offspring survival (Mumme 1992; Mitani & Watts 1997; Thompson *et al.* 2019) and offspring reproduction (Russell *et al.* 2006). Types of alloparental care vary between species as well as within a species and include both direct and indirect investment in offspring survival and growth. Indirect alloparental care refers to behaviours which are not directed at the young but still affect their survival; such care includes sentinel behaviour, territory defence and shelter construction and maintenance (Kleiman & Malcolm 1981). Direct forms of alloparental care are interactions with the offspring such as allosuckling, babysitting, feeding, grooming, moving and group-sleeping.

1.2.1 Allosuckling

Allosuckling is where females nurse another female's young and is most commonly seen when the female is also nursing her own young (Gittleman & Thompson 1988; Packer *et al.* 1992). In monotocous species (species which give birth to one individual), allosuckling is usually associated with 'milk theft', consequently mothers have evolved the ability to identify their own offspring to reduce the likelihood of this occurring (Bartholomew 1959). However, in polytocous species (species which birth multiple offspring), 'milk theft' can be seen in species which live in groups where there is less selective pressure to discriminate their own offspring (Fullerton *et al*. 1974) and because of their high relatedness, allonursing could increase the female's inclusive fitness (Hayes 2000). Within social mammals there is substantial variation in the amount of allonursing which occurs, which could be due to variation in external threats and the costs associated with nursing non-offspring (Pusey & Packer 1994). In lions, it is suggested that allonursing in females is a by-product of communal defence against infanticide and because they spend longer periods of time with cubs, allosuckling is more likely to occur (as cubs have more opportunity to sneak suckle other females) compared to species where females spend less time with the offspring (Pusey & Packer 1994).

Allonursing is energetically costly for the lactating female; in 10% of all species where allonursing has been observed, non-offspring were nursed as much as the female's own young (König 2006). This type of cooperative care was initially assumed to be maladaptive for the nursing female; in rodents it was believed to be a forced behaviour which is a cost to communal living (Hayes 2000). However, potential adaptive benefits have been found. In bats, allonursing may increase female foraging success by reducing weight before hunting (Wilkinson 1992). Furthermore, in dwarf mongooses, Rood (1980) proposed that allonursing enhances the chance of offspring survival if the dominant female dies.

1.2.2 Babysitting

Babysitting is when young are guarded by adults; group members share responsibility for babysitting when the rest of the group leave to forage. Babysitting has been documented in many social mammals,

including sperm whales (*Physeter macrocephalus*) (Whitehead 1996), banded mongooses (Cant 2003), dwarf mongooses (Rood 1990) and meerkats (Clutton-Brock *et al.* 2000). The benefit of babysitting is that it allows the mother to increase her foraging time, and therefore her milk supply, without increasing predation risk to their offspring. The foraging behaviour of the group has a direct influence on the cost which can be accrued to the babysitter. In meerkats, babysitters can lose up to 1.3% of their body mass in one babysitting bout by remaining with the pups (Clutton-Brock *et al.* 1998). However, in marine mammals such as sperm whales, babysitters suffer less cost because they adjust their dive synchrony to account for an adult to remain with the calf (Whitehead 1996). Moreover, in the Cape Breton population of pilot whales (*Globicephala melas)*, there is little observable cost associated with babysitting (Augusto *et al.* 2017) which suggests that this could be a by-product of their social structure. Therefore, the current literature suggests terrestrial mammals could pay greater costs than marine mammals in babysitting activities as it reduces their foraging time.

1.2.3 Feeding

When young begin to eat solid foods, group members can assist with feeding them before they are able to forage and/or hunt independently. Research by Thompson *et al.* (2019) on wild habituated banded mongooses found that pups which received more care had an earlier first oestrus, therefore feeding by other group members significantly affects the survival and reproductive success of the pups. Group size could significantly affect feeding investment in cooperatively breeding mammals (Creel & Creel 1991; Clutton-Brock *et al.* 2000) which in turn influences offspring growth rates. Meerkat feeding contributions are significantly influenced by the foraging success of the helper as well as their age and sex (Clutton-Brock *et al.* 2001); this suggests there are many factors involved which govern levels of feeding investment in cooperatively breeding terrestrial mammals. Being exposed to prey items is vital for the growth and survival of young. In meerkats, adults adjust the prey items given in response to the pups' feeding abilities and it has been proposed that adults teach pups how to handle live prey, which could increase the efficiency of information transfer (Thornton & McAuliffe 2006). Consequently, not

only is feeding vital for increased probability of survival and reproduction, but it can also enhance the offspring's hunting capabilities in a shorter amount of time through exposure to novel prey items.

1.2.4 Grooming

Grooming serves a host of functions which benefit group members and is commonly seen in many group-living species (Spruijt *et al.* 1992; Silk *et al*. 2003). Within social groups, grooming investment varies between individuals; for example, in social primates, group members preferentially groom either high-ranking individuals or close kin (Schino 2001) and the strongest grooming bonds tend to be between mothers and daughters (Missakian 1974). In vampire bats (*Desmodus rotundus*), social grooming is thought to facilitate food sharing by recognition of kin before regurgitation (Carter & Leffer 2015). However, in impala (*Aepyceros melampus*), grooming is believed to be a form of reciprocal altruism whereby dominants do not receive more grooming than subordinates (Hart & Hart 1992).

The grooming of young by helpers is frequently observed in many obligate cooperatively breeding groups (Kutsukake & Clutton-Brock 2006; Waterman & Roth 2008). Offspring grooming has been found to play an important role in offspring social development. In a laboratory study on Long-Evans hooded rats (*Rattus norvegicus domestica*), the offspring of mothers which groomed at a higher rate had reduced hypothalamic–pituitary–adrenal endocrinological stress reactivity as adults (Liu *et al.* 1997). Moreover, female offspring were more likely to exhibit similar levels of parental care which demonstrates the trans-generational benefits of grooming behaviour during offspring development. Little work has been done on the long-term benefits of allogrooming in wild populations, however the assistance of helpers in the cooperatively breeding banded mongoose has been found to increase offspring survival and reproductive success (Vitikainen *et al*. 2019) which could be influenced by grooming interactions.

1.2.5 Moving offspring

Many social mammal groups live in territories which are defended by conspecifics for exclusive access to resources. To maintain these territories, it is vital to undergo defensive behaviours which can range

from being visual and vocal to the use of olfaction (Christensen & Radford 2018). However, when offspring are born, they can have a significant impact on the group's movement capabilities which not only reduces the area that the group can forage in but also reduces their ability to undergo these defensive behaviours. Therefore, moving offspring is important for group feeding as well as maintaining territories, although moving offspring between burrows is a costly behaviour because it increases offspring predation risk (East *et al.* 1989; Ausband *et al.* 2016) and is energetically demanding for the carer (Sánchez *et al.* 1999). When multiple offspring are born in groups of obligately cooperative breeders, helpers are likely to assist with the movement of offspring to maintain group cohesion (Silk 2007), but there has been little research on which group members assist with the movement of offspring.

1.2.6 Group sleeping

It is well known that thermoregulation (in the form of group sleeping) is important for the survival of young of species which live in cold climates (Madison 1984; Arnold 1993). For example, juvenile marmots (*Marmota*) which undergo hibernation require adults to regulate their arousal cycles as well as to reduce their energy stress during these periods (Blumstein & Armitage 1999). Vervet monkeys (*Chlorocebus pygerythrus*) with stronger social bonds have higher thermal competencies compared to individuals with fewer social partners (McFarland *et al*. 2015). However, in cooperatively breeding mammals which live in hot climates, group sleeping is unlikely to occur for thermoregulatory benefits, suggesting that it has other benefits (Eberle & Kappeler 2006). In dwarf mongooses, for instance, there are high rates of grooming during group sleeping bouts (Emily Grout personal observations), suggesting it is also strengthening social bonds (Kern & Radford 2016, 2018). Furthermore, if young individuals are kept in the centre of the huddle during group sleeping, this behaviour could also be a form of protection.

1.3 Variation in alloparental care

In obligate cooperative breeders, there is considerable variation in alloparental care between populations (Roberts *et al*. 1998; Gero *et al*. 2009; Whitehead *et al*. 2012), but especially between individuals due a variety of factors.

1.3.1 Relatedness

Hamilton's theory of kin selection predicts that individuals which have a higher relatedness to offspring are more likely to invest in alloparental activities to increase their inclusive fitness (Hamilton 1964; Brown 1987). There is evidence for this hypothesis in natural populations; for instance, in wedge-capped capuchin monkeys (*Cebus olivaceus*), female siblings interacted with kin four times more than female non-kin (Robinson & O'Brien 1991). Additionally, a comparative analysis of relatedness and allomaternal care from 44 mammal species conducted by Briga *et al*. (2012) discovered that there is a positive association between allomaternal care and relatedness. However, in chimpanzees, high relatedness in the philopatric group is only observed in small groups (Lukas *et al*. 2005), which suggests alloparental behaviours may not be driven by relatedness in larger groups.

1.3.2 Sex

There are multiple theories as to why there are differences in alloparental investment between the sexes of cooperatively breeding mammals. Differences in alloparental care between males and females could depend on the varying opportunities to inherit a territory when the breeding pair dies (Cockburn 1998). However, in meerkats, there was no evidence that females adjusted their level of helping behaviour to increase their probability of becoming a dominant and hence inheriting a territory (Duncan *et al.* 2018). From chromosomal analysis, it is theorised that female mammals will do the majority of offspring care because beneficial rare genes will be passed on through the female sex chromosome (Hudson & Shellman-Reeve 1997). However, the social organisation of the group could also have an effect on the sex-bias variation in helping behaviour. In meerkats, females have been found to contribute more to the rearing of young (Clutton-Brock *et al*. 2002). In addition, research on the Damaraland mole rats

(*Fukomys damarensis*) found that both sex and breeding status influenced the level of helping; breeding females were more likely to carry pups compared to non-breeding females, whereas non-breeding males were more likely to carry pups compared to breeding males (Zöttl *et al.* 2018). Therefore, it is likely that there are multiple factors influencing whether females or males invest in alloparental behaviours.

Mullon *et al*. (2014) showed that sex differences in mortality will affect the strength of selection for male or female investment in care. Recent research on banded mongooses has found ecological variation could cause changes in sex bias in alloparental care (Marshall *et al*. 2016). Females were found to be more sensitive to high levels of rainfall leading to male-biased groups, which in-turn increases male helping behaviour. Previous research on banded mongoose alloparental care supports this finding; Hodge *et al.* (2007) found males helped more than females in pup care. They hypothesised that this difference was due to differences in the cost associated with pup care; males would incur a reduced future reproductive cost compared to females. Woodroffe & Vincent (1994) hypothesised that male care could allow females to produce a greater number of energetically costly offspring, which could be vital under particular ecological and social conditions for group survival. A study by Malcolm & Marten (1982) on wild dogs found that there was a male-biased sex ratio in groups and more male helpers increased the likelihood of pups surviving. Further study found that the addition of extra males in the group increased hunting success (because they are communal hunters) which consequently increased pup survivorship by provisioning the gestating female (Gusset & Macdonald 2010). Therefore, male helpers might be indirectly benefitting pup survival as a consequence of their hunting strategies.

1.3.3 Age

The cost of helping can vary significantly between group members of different age; older individuals being more likely to have greater efficiency in finding food as well as improving their alloparental skills as they gain experience with age. Clutton-Brock *et al*. (2000) found that adults contributed significantly more than juveniles in the cooperative care of young in meerkats. Moreover, meerkat pups are more likely to follow older adults in the group, suggesting they have greater foraging efficiency (Brotherton

et al. 2001). Greater contributions by adults has also been found in the African striped mouse (*Rhabdomys pumilio*), where one study found 24% of care was given by subadults whereas 6% was given by juveniles (Rymer & Pillay 2014). By contrast, in the wedge-capped capuchin monkey, subadult and juvenile females were found to invest more in alloparental activities compared to adult females (O'Brien & Robinson 1991).

1.3.4 Dominance status

There is a delicate trade-off between the amount of care helpers will give compared to the breeding pair. In social groups which have a dominant breeding pair and subordinate adults which assist in the rearing of offspring, there are many factors which influence the amount of assistance the subordinates invest in the dominants' young; these factors include the dominant pair's investment in pup rearing, the likelihood of the dominant pair surviving to the next breeding season as well as the risk of being evicted from the group for lack of alloparental care duties (Kokko *et al.* 2002). The assistance of subordinate helpers is likely to increase the survival and reproductive success of the dominants by decreasing their caring efforts (Hatchwell 1999), which could reduce the probability of subordinates reaching dominance status. Individuals which have a higher dominance status have been found to be more generous in altruistic acts; De Waal (1989) found chimpanzees that had higher ranks were more generous in sharing their food which suggest higher quality individuals are able to behave altruistically at a smaller cost. De Waal also found that high-ranking females interacted with infants more than low-ranking females. This shows that dominance status could significantly affect variation in alloparental behaviours between group members.

1.3.5 Helper quality

In mammals which are not obligate cooperative breeders, the assistance of helpers is likely to increase offspring survival (Macdonald 1979; Moehlman 1979). Despite this, a study on cooperatively breeding in the European badger (*Meles meles*) has found that helpers had a negative effect on the reproductive success of mothers, and that mothers with helpers were in a worse condition than those without helpers

at the end of the breeding season. These helpers were sexually mature, and it is likely that they failed to breed from high competition for resources and hence assisted with the rearing of close relatives' young, despite having poor health (Woodroffe & Macdonald 2000). Therefore, the quality of the helper is likely to affect their ability for increasing offspring survival.

Alloparental care is a costly behaviour, and therefore the amount of care given is flexible which could be dependent on the quality of the helper (Heinsohn 2004). As previously discussed, meerkat babysitters lose up to 1.3% of their body mass during a babysitting bout (Clutton-Brock *et al.* 1998) and are sensitive to group-size changes, modifying their investment accordingly. Helpers will increase their helping effort when the number of helpers in the group is reduced (Kutsukake & Clutton-Brock 2006). However, the quality of the helper has not been found to affect their alloparental investment when the cost to help is high (Clutton-Brock *et al.* 2004). Conversely, research conducted by Bell (2008) on banded mongooses found that helpers in good condition would respond to pups more compared to helpers in poor condition and pups would strategically adjust their begging effort towards higher quality helpers. Research on banded mongooses had also found that, unlike meerkats, their group size did not influence the level of alloparental investments (Gilchrist & Russell 2007), rather the probability of breeding in the following year was more likely to affect whether adults became helpers.

1.3.6 Social-bond development

Banded mongooses exhibit a unique pup–escort relationship where the escort feeds and grooms one pup significantly more than the other pups (Gilchrist *et al*. 2008). The evolutionary benefit for developing these strong social bonds could be to increase the adult's inclusive fitness by helping related pups. However, pups which had an escort were more likely to survive during the association period compared to non-escorted pups, suggesting both the adult and the pup could be benefitting from the escort relationship.

One of the most consistent behavioural traits found in primates is female care of non-offspring (Paul 1999), which will likely develop female social bonds with offspring. Furthermore, male–male social bonds are commonly seen in primates (Newton-Fisher 1999; Buchan *et al*. 2003) and research

on spider monkeys (*Simia paniscus*) has found that adult males will preferentially care for male infants (Evans *et al*. 2012). This sex preference is suggested to help develop their social bonds with potential future allies because spider monkeys are a highly cooperative species. Moreover, social bonds between the breeding pair and their helpers has been found to contribute to the helpers' investments in alloparental activities. For example, adult marmosets which have strong affiliative relationships with the main caregivers contributed more to offspring care (Finkenwirth & Burkart 2018).

1.3.7 Preferential care

There has been limited research on preferential care between offspring after birth, with most research conducted on obligate cooperative breeders. Mathematical modelling by Lessells (2002) found that helper preferences towards particular offspring can be explained by differences between individuals in the benefits of caring for a particular type of offspring. As discussed above, there is evidence that adult banded mongooses can preferentially care for particular pups. Though these pup–escorts dyads were originally believed to be controlled by the pup (Gilchrist 2004), there has been further research which has shown that escorts were more likely to respond to the pup whom they were escorting (Gilchrist *et al.* 2008), suggesting that helpers could be preferentially investing in alloparental behaviours of particular individuals.

Offspring sex can influence which helpers care for which offspring. In meerkats, female offspring are preferentially cared for by both helper sexes compared to male offspring (Brotherton *et al*. 2001). However, in banded mongooses, Vitikainen *et al*. (2017) found that there was clear assortment of sex between the helpers; female helpers were more likely to tend to female pups and male helpers to male pups. In meerkats, caring for female pups is preferred because they are less likely to emigrate from their natal group (Brotherton, *et al*. 2001; Clutton-Brock, *et al*. 2002), but in banded mongooses, there is no distinctive difference between the sexes in their likelihood of emigrating (Cant *et al.* 2001). Despite there not being a difference in emigration probability between the sexes, female banded mongoose pups which receive more care had higher reproductive success (Thompson *et al*. 2019), which suggests helpers could gain greater inclusive fitness by preferentially caring for females.

In conjunction with this, Bell (2008) found that banded mongoose escorts were more responsive to female pups that begged at a higher rate.

Relatedness is likely to influence which offspring receive preferential care. Research on a semi-free-ranging population of barbary macaques (*Macaca sylvanus*) has found that mothers are able to recognise the vocalisations of their own offspring, which suggests adults could be able to adjust their contributions to alloparental behaviours depending on their level of relatedness. In groups which have high variance of relatedness, kin discrimination is more likely to occur to increase helper's indirect fitness benefits (Cornwallis *et al*. 2009). However, in social groups which have high levels of in-group relatedness, there is less pressure for kin discrimination to evolve (Griffin & West 2003).

1.4 Dwarf mongoose background

Dwarf mongooses are diurnal, cooperatively breeding mammals that inhabit wooded savannahs in south and east Africa. Groups of 5–30 individuals consist of a dominant breeding pair and subordinate helpers of both sexes, which include more than one generation of offspring as well as a smaller proportion of unrelated male and female immigrants (Rood 1983; Kern & Radford 2018). Average life expectancy is 3–4 years, yet some individuals have been reported to live for over 10 years (Rood 1987); groups include individuals of various ages. Group members sleep (most commonly in termite mounds), forage and move together throughout the day, as well as scent-mark at communal latrines. Groups are highly territorial and will physically defend their territory against rivals (Morris-Drake *et al.* 2019). Movement between groups occurs infrequently, however it is most likely to occur during the breeding season, with males being the more common dispersing sex (Rood 1987).

The main source of food for dwarf mongooses is invertebrates, which are dug up from the substrate (Rasa 1989). During the dry season (May to October in South Africa), foraging occurs throughout the day; in the rainy season (November to April), the majority of foraging occurs in the early mornings and late afternoons (when it is cooler) and the group will rest in shaded areas during the hottest periods of the day. Dwarf mongooses perform anti-predator defensive behaviours in the form of mobbing, alarm calling and sentinel activity (Rasa 1989; Kern & Radford 2013, 2014, 2016). They also

groom one other frequently (Rasa 1977; Kern & Radford 2018) which likely serves a host of benefits such as removing ectoparasites, reducing stress levels and maintaining social bonds (Aureli & Yates 2009; Russell & Phelps 2013). Furthermore, recent research on dwarf mongooses by Kern & Radford (2018) has found grooming behaviour is used as a tradable commodity for sentinel behaviour.

As seasonal breeders, dwarf mongooses have two to three litters consecutively, with the first litter born at the start of the rainy season (usually late October in South Africa). The dominant female does not reproductively suppress other females in the group however it is unknown whether the subordinate females' pups survive after she has given birth to them. It has been suggested that the dominant female does not reproductively supress other females because having additional lactating females in the group can also feed her offspring, which allows the dominant female to build up more reserves for the next litter (Creel & Waser 1991). All group members engage in pup rearing (Jennions & Macdonald 1994), including a range of alloparental behaviours (e.g. feeding, grooming and group-sleeping).

Dwarf mongooses are an ideal study system to research alloparental care because they reproduce at a high rate with short generation times (Rood 1987). They can also be easily habituated within <5 m proximity by observers on foot (Kern & Radford 2013) so detailed behavioural observations can be made. Furthermore, they can be dye-marked which allows for individual identification (Kern & Radford 2013). Previous studies on alloparental care in dwarf mongooses have found conflicting results. Rasa (1977) found that the majority of care was exhibited by the dominant male and older siblings, whereas Rood (1978) found that most care was provided by subordinate females, in particular the younger individuals. Since then, there has been no further study on variation between individuals in their level of caring investment towards pups, therefore this study will build upon the growing literature in alloparental care.

1.5 Thesis aims

Whilst there is considerable evidence for variation in alloparental care within cooperatively breeding mammals, research in the field has been limited to a small number of species and little work has

analysed whether there is variation between individuals in different caring tasks. Disparities are seen between species on the factors which influence helper contributions to pup care, which is likely due to differences in selective pressures driving cooperative care. The current study therefore contributes to the literature on alloparental variation. Here I examined variation in alloparental tasks of adult individuals in a wild habituated population of dwarf mongooses. Previous studies on alloparental care in this species has found conflicting results, the first study conducted by Rasa (1977) found that most of the care was from the dominant male and older siblings (Rasa 1977), however Rood (1978) found the majority of care was given by younger females. Since then, there has been no research on variations in dwarf mongoose adult contributions to pup care. Hence this study aims to build on the current literature on alloparental investments with the hope of furthering our understanding of the factors which influence caring activities by helpers.

Chapter 2: Variation in alloparental investment in dwarf mongooses

2.1 Abstract

Alloparental care (the provision of care to offspring by adults other than the parents) is widespread in social vertebrates. However, there is much unexplained variation in the contributions of different group members to these helping activities. Dwarf mongooses (*Helogale parvula*) live in groups of 5 to 30 individuals, consisting of a dominant breeding pair and subordinate adult helpers of both sexes. All adults contribute to feeding, grooming and group-sleeping with the young. I used detailed observations from seven wild but habituated dwarf mongoose groups to examine whether sex, dominance status and age influence variation in alloparental care. I found that subordinates, especially younger individuals, fed pups more frequently than dominants, but dominants brought larger prey items than subordinates. Subordinate females groomed pups more frequently than dominant females, but there was no difference in grooming frequency between dominant and subordinate males. Additionally, subordinates groomed pups for longer durations than dominants. I found no evidence that male or female helpers preferentially feed or groom pups of a particular sex. Furthermore, there was no significant difference between helpers in group-sleeping bouts. To test whether adults preferentially feed certain pups, a playback experiment using pup begging calls was designed, and pilot trials conducted. Preliminary results indicated that neither sex nor age of subordinate group members influenced their mean response latency to respond to different begging tracks, but a full experiment would be needed for strong conclusions. In summary, I found that there is variation between group members in their level of investment in different alloparental tasks. Therefore, future studies on variation in alloparental behaviour should consider multiple caring activities exhibited by group members to obtain a broader understanding of the factors involved, and to extend our understanding of cooperation, parental care and social living.

.

2.2 Introduction

Cooperative breeding is the social system whereby a breeding pair are helped to raise their offspring by non-breeding group members (known as helpers). It is found in a variety of taxa including mammals, birds, fish and invertebrates (Jennions & Macdonald 1994; Stacey & Koenig 1990; Emlen & Vehrencamp 1983; Wisenden 1999; Klepzig & Taborsky 2011; Koenig & Dickinson 2016). Members of cooperatively breeding groups help in many ways, including with territory and anti-predator defence (Koenig & Mumme 1996), increasing foraging success (Jennions & Macdonald 1994), grooming other members (Lazaro-Perea 2004) and alloparental care. Alloparental care is when individuals other than the breeding pair provide direct assistance in raising the offspring, which includes behaviours such as suckling, feeding, grooming and babysitting the young (Riedman 1982). Previous research has shown that groups which exhibit alloparental behaviours have greater young survival rates (Mumme 1992; Mitani & Watts 1997; Thompson *et al.* 2019), demonstrating the benefit of this behavioural strategy.

Variation between group members in their level of alloparental investment has been widely studied in birds (Green *et al*. 2016; Kingma 2017) and mammals (Clutton-Brock *et al*. 2000; Perkeybile *et al*. 2015; Vitikainen *et al*. 2017; Zöttl *et al*. 2018). Most studies have considered how differences in relatedness, sex, age and body condition of helpers affect the level of caring behaviour. In meerkats (*Suricata suricatta*), for instance, there is clear division in helping effort between the sexes with females feeding pups significantly more than males (Brotherton *et al.* 2001). Whilst the level of contributions to caring activities in meerkats does not correlate with relatedness, younger individuals contribute more to pup feeding than do older individuals (Clutton-Brock *et al*. 2001, 2003). Furthermore, a supplementary feeding experiment conducted by Clutton-Brock *et al*. (2001) revealed that helpers who were fed additional food fed pups significantly more, suggesting that the condition of helpers affects alloparental contributions. Banded mongooses (*Mungos mungo*) exhibit an escort care system where an adult will care for one pup significantly more than other pups (Gilchrist *et al*. 2008); female helpers are more likely to care for female pups and male helpers for male pups (Gilchrist *et al*. 2008). Relatedness does not explain adult–pup associations in banded mongooses (Vitikainen *et al.* 2017), but individuals who are less than a year old increase their caring investment with age and body weight (Gilchrist &

Russell 2007). However, the biggest determinant of caring contributions in banded mongooses is whether an individual has bred: breeders invest more in escorting than individuals who have not bred (Gilchrist & Russell 2007).

Although variation in alloparental investment in cooperatively breeding mammals has been studied, most research has focused on one type of alloparental task (Clutton-Brock *et al.* 2000; Gilchrist & Russell 2007; Augusto *et al.* 2017), with a limited number of studies focusing on variation between tasks. In meerkats, for example, Clutton-Brock *et al.* (2004) found differences in contributions between tasks which could be dependent on variation in costs and benefits associated with the different helping behaviours (babysitting and feeding). Females babysat and fed pups more than males, whereas males exhibited more anti-predator behaviours than females (Clutton-Brock *et al.* 2004). By contrast, Thorley *et al*. (2018) found no task specialisation in Damaraland mole-rats (*Fukomys damarensis*) when considering 16 different behaviours (which included feeding, carrying and nest building). However, overall contributions to caring tasks varied with age and relative size of group members (Thorley *et al*. 2018). These studies demonstrate that there can be variation between species in task specialisation, therefore future studies should consider multiple types of activities conducted by helpers, and an expansion of the species considered will be valuable.

Like meerkats and banded mongooses, dwarf mongooses (*Helogale parvula*) are cooperatively breeding mammals in which all group members engage in pup rearing (Jennions & Macdonald 1994), including a range of alloparental behaviours (e.g. feeding, grooming and group-sleeping). Food items are given throughout the day by most group members whereas grooming and group-sleeping occur most frequently when the group is at rest (usually at the sleeping burrow) (Emily Grout personal observation). However, unlike meerkats and banded mongooses, dwarf mongoose variation in alloparental care has had little attention in the scientific literature. As there are clear differences between meerkats and banded mongooses in the types of alloparental care they exhibit, analysis of this variation in dwarf mongooses will expand our knowledge on the evolution of cooperative care. Studying variation in dwarf mongoose alloparental contributions is made easier because wild dwarf mongooses can be habituated to the close presence of observers (Kern & Radford 2013, 2014, 2016, 2018), which allows detailed examination of the various caring behaviours group members exhibit in natural conditions.

Here we examined how dominance status and sex of all group members, as well as age and body condition of subordinates, affect variation in contributions to multiple alloparental behaviours in dwarf mongooses. Detailed observational data were collected, from seven habituated groups of wild dwarf mongooses, on feeding, grooming and group-sleeping interactions between adults and pups. We predicted that dominant individuals would invest less in alloparental activities compared to subordinate individuals and that dominant female would invest less than the dominant male because she would be building up reserves in preparation for the next litter. We also predicted that subordinate males would invest less than subordinate females in alloparental tasks because males are more likely to emigrate from the group (Rood 1987; Creel & Rabenold 1994). We predicted that younger individuals would be more likely than older individuals to invest in all alloparental activities because they are more likely to be siblings of the new litter, and therefore would be maximising their inclusive fitness by assisting in their development. We also predicted that individuals in better quality body condition would invest more in pup caring tasks. Furthermore, we trialled a field-based playback experiment designed to test whether particular adults show preferential care towards particular pups (as observed in banded mongooses).

2.3 Methods

2.3.1 Study species and population

Dwarf mongooses are cooperatively breeding mammals distributed in south and east Africa. They live in groups of 5 to 30 individuals, consisting of a dominant breeding pair and subordinate helpers of both sexes (Rood 1983; Kern & Radford 2018). They are seasonal breeders, having two or three litters consecutively, with the first litter born at the start of the rainy season (usually late October). After birth, pups remain inside the sleeping burrow for 10–14 days; typically, adults take turns in babysitting the pups at this age when the group leaves the burrow to forage. The dominant female, and in some groups the subordinate female, suckle the pups during lactation. When pups begin to emerge from the sleeping burrow, the adult group members will forage in close proximity, bringing prey items to the pups. Adults will repeatedly return to the pups to groom and scent-mark them as well as to rotate the babysitting role.

When the group is at rest, which is usually during the hottest time of the day, the adults will sleep with the pups.

I collected observational data and conducted a pilot experiment at the Dwarf Mongoose Research Project (DMRP) at Sorabi Rock Lodge, Limpopo Province, South Africa (24° 11′S, 30° 46′E) from October until December 2018. This region is in the savannah biome (Rutherford *et al.* 2006), categorised by two distinct seasons: summer which is hot and wet (September to April) and winter which is cold and dry (May to August). Full details of the study site are available in Kern & Radford (2013). The DMRP monitors eight groups of wild dwarf mongooses, which have been habituated to the close presence (<5 m) of observers on foot (Kern & Radford 2013). For this study, data were collected from seven of these habituated groups (mean adult group size ± SE: 12.5 ± 4, mean litter size ± SE: 3.4 ± 1.5). Permission for this study was given by the Ethical Committee of Pretoria University, South Africa, the Ethical Review Group of the University of Bristol, United Kingdom (University Investigator Number: UIN/17/074), and the Department of Environmental Affairs and Tourism, Limpopo Province, South Africa (permit number: 001-CPM403-00013).

From ongoing behavioural research on this population of dwarf mongooses since 2011, all adults have been identified, sexed and the majority have been aged (Kern & Radford 2013, 2014, 2016, 2018). All individuals are distinguishable either from blonde hair-dye marks (Wella UK Ltd, Surrey, U.K.), applied to their fur with an extended paintbrush, or from recognisable face and body scars. Pups were dye-marked within 3 days of leaving the sleeping burrow to allow discrimination between individuals. The dominant breeding pair can be identified from aggressive behaviours, foraging displacements and grooming interactions (Rasa 1977). Individuals are trained, using small amounts of hard-boiled egg, to stand on a balance scale. Weights are collected three times a day — before the group leave their sleeping burrow in the morning, at least 3 h after foraging, and when the group are at their sleeping burrow in the evening — and were used to estimate adult foraging success and to determine whether this affected pup-feeding investment.

2.3.2 Observational data collection

To assess variation between adults in pup-care activities, adult–pup interactions were recorded from the first litter of the season of seven groups. All interactions were recorded on an *ad lib* basis until all interactions were unable to be observed simultaneously, which occurred when the pups became more independent, approximately 4 weeks after birth. When all feeding, grooming and group-sleeping interactions with adults could not be recorded, focal watches were conducted on pups, recording all these interactions which occurred to one pup during a 25 min period. If an interaction between a different pup and an adult was observed during a focal watch, this was also recorded *ad lib*. The order in which the pups were focal-watched was randomised during each observation period. In each group, at least one focal watch per pup was conducted in each observation period, unless the observation period was terminated early due to heavy rainfall and thunder (resulting in the group moving into a sleeping burrow). Morning observation periods lasted 4–5 h; afternoon observation periods were approximately 3 h in duration.

Several alloparental behaviours exhibited by dwarf mongooses once pups are old enough to leave the burrow were recorded in this study: feeding, grooming and group-sleeping (Figure 2.1). For pup-feeding, the time of the feed was recorded as well as the identity (ID) of the adult providing the food and the pup who received the food item. A four-point scale was used to categorise the size of the food: small = > 90% of the food item inside the adult's mouth; medium = > 50% of the food item inside the adult's mouth; large = > 50% of the food item visible outside the adult's mouth; and extra-large = > 90% of the food item outside the adult's mouth. For pup-grooming, the ID of the adult and the pup involved were recorded as well as the duration of the grooming bout. Group sleeping is when at least one adult holds at least one pup in their abdominal region; group-sleep sizes varied from one adult up to most of the group. All adults who were sleeping with direct physical contact with the pups in the group-sleep were recorded, as well as the duration that each adult spent in the group-sleep.

Figure 2.1. Images of the different alloparental behaviours that adult dwarf mongooses exhibit and for which data were collected. (A) Foraging for a prey item to feed to a nearby pup. (B) Grooming. (C) Group-sleeping. All images were taken by Emily Grout.

2.3.3 Observational data analysis

Mixed models were constructed in RStudio 3.5.2 (R Development Core Team 2018) whereas the other statistical tests were run using IBM SPSS Statistics for Windows version 25 (IBM Corp 2017). All tests were considered as significant at $p < 0.05$. Generalised linear mixed models (GLMMs) and linear mixed models (LMMs) were used to include fixed and random factors in the same models (package: lmer4; (Bates *et al*. 2014)); random factors allow control for repeated sampling from the same individuals and individuals in the same groups. Fixed factors were adult sex (male and female), dominance status (dominant and subordinate) and age (2 years and older and younger than 2 years). Since dominant individuals are likely to be older than subordinates (Rood 1990), and thus dominance status and age are likely strongly correlated, analyses of age were restricted to subordinate individuals. Random factors were adult ID and group ID. For the maximal model, all explanatory terms and the 2-way interactions of these terms were included. Stepwise deletions of terms which were non-significant (Crawley 2007) was conducted using the drop1 command (using the lmerTest package version 3.5.3) to determine the minimal model. To distinguish which model best fit the data, comparisons of Akaike Information Criterion (AIC) were completed. LMMs (with a Gaussian distribution) were run for data on subordinate feed frequencies. Otherwise, Gamma GLMMs were run as data did not fit the assumptions of parametric testing. The Gamma distribution was used because it can deal with heteroskedasticity in non-negative

continuous data. Each model was fitted with the link which best fit the data; the link used for each model is included in the output tables.

Difference in subordinate adult body mass before and after pup emergence was calculated from the mean weight of adults within a 14-day period before the pups were born and the mean weight of adults in the 14 days after the pups in their group were first observed to forage independently. Dominants were not included because females in particular show large weight changes related to breeding at this time of year. Ten female and 14 male subordinate adults were excluded from the analysis because there were no weights recorded for either or both of the relevant time periods. Data were therefore available for 50 subordinate adults (27 females and 23 males). Since body mass difference between pre- and post-pup emergence did not significantly affect feeding and grooming interactions (see Results), it was not included as a random variable in subsequent GLMMs.

For pup-feeding behaviour, data from 80 adults were used in the analysis of dominance and sex, and 53 adults were used in the analysis of age and sex of subordinates. Four adults were removed from the analysis because they were not observed to feed the pups during the total observation period. Grooming frequency data from 81 adults were used in the analysis of dominance and sex, and 54 adults were used in the analysis of age and sex of subordinates. Three individuals were removed from the analysis because no grooming was observed by these individuals. For group-sleeping, data from 50 adults were analysed; groups which had less than a total of eight group-sleeping bouts recorded were not included in the analysis.

2.3.4 Pilot experiment - Adult responses to pup begging

To test which adults responded to the pups and whether they had a preference for a particular pup, a playback experiment was designed. Due to logistical and time constraints, only pilot trials were conducted in one of the mongoose groups which had two pups (of the same sex) in the first litter of the season; trials took place within a five-day period. When the pups are predominantly being fed by group members (30 days after birth), they are very vocal, begging throughout most of the day when adults are foraging (Emily Grout personal observation). Begging calls were recorded from identified pups using

a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ) and a Sennheiser directional microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK). The sampling rate of the recordings was of 48 kHz with a 24-bit resolution, and recordings were stored on a Transcend SD card (Transcend, Taipei, Taiwan). Recordings were made in calm weather conditions within 1–2 m of the focal pup when it was at least 5 m from the other pups to ensure that only the begging calls of the focal pup were recorded. To ensure that the pups were at a similar hunger level when recorded, recordings were made within 1 h of each other.

Audacity (version 2.3.0) was used to remove loud background noise from the recordings (using a high-pass filter; 9000 Hz, 12 dB per octave) and to make 5-min tracks for each pup; tracks contained the same rate and amplitude, to ensure that there were no differences in the begging strength. Resulting playback tracks were downloaded onto RUIZU MP3 players, one track per MP3 player. A HandyMAN TEK 1345 sound meter (Metrel UK Ltd., Normanton, UK) was used to measure the peak sound-pressure level of the begging calls (in dB) to ensure the playback volume was standardised to the volume of natural begging calls.

Playback trials were conducted in still weather conditions, after the group had left the sleeping burrow, when most of the group were foraging and before the group returned to the sleeping burrow in the evening. Trials took place when there had been no group disturbances for at least 15 min. Before the playback experiment, most of the group had to be at least 15 m from the pups, so that begging calls from the pups themselves did not interfere with the playback experiment. Small amounts of hard-boiled egg were thrown to attract group members into the area. Two Rokono B10 BASS mini Bluetooth speakers were placed 2.5 m apart, on each side of the observer, hidden in the vegetation with the connected MP3 players placed below the observer. The begging-call tracks were played from both speakers simultaneously, 2 min after the egg was thrown. The ID of the adults in the experiment area were recorded.

The ID of the adult individuals that responded to the playback, time till response and the ID of the speaker to which each adult responded were recorded. If the adult responded to both speakers, each response was recorded. Behaviours which were classified as a response included looking at the speaker, approaching the speaker and sniffing the speaker. If the group began lost calling or behaved in a

distressed manner (e.g. alarm calling, multiple individuals becoming sentinels), the playback was stopped. To reduce probability of the group habituating to the track, the playback was repeated no more than once per hour. Trials were repeated 12 times to the same group (group size = 14 adults); To assess mean response latency to each speaker, Mann-Whitney U tests were run. Mann-Whitney U tests were also run to compare whether sex and age of subordinates affected mean response latency. Due to conducting the experiment to one group, the small sample size of dominant individuals did not allow for analysis between dominance status in response latency, however qualitative results are presented.

2.4 Results

Dwarf mongooses typically have two to three litters during the rainy season (Rood 1980), with the first litter born in October. In this study, 11 females gave birth in seven groups in the first litter. All dominant females were pregnant, and in four of the seven groups, the oldest subordinate female was also pregnant. In the first litter, 24 pups were born (4 died before being sexed), the mean number of pups born per group was 3.4 (9 males : 11 females). The mean (± SE) group size of all individuals excluding pups was 12.4 ± 4.0. The mean number of adults older than 2 years was 5.8 ± 2.3 per group and the mean number of adults less than 2 years old per group was 6.6 ± 1.5. The mean number of females (excluding pups) per group was 6.2 ± 2.4 and the mean number of males (excluding pups) per group was 6.2 ± 2.9. Table 2.1 provides a summary of the number of feeding, grooming and group-sleeping observations collected for each group.

Table 2.1. Total number of feeding, grooming and group-sleeping observations recorded from the first litter of pups in seven dwarf mongoose groups. The total observation time (mins) and the number of pups which emerged is included.

Mongoose group	Number of emerged pups	Total observation time (mins)	Total number of feeds	Total number of grooming bouts	Total number of group-sleeping observations
Half Pints	5	4329	470	340	47
Bookworms	3	5053	561	654	43
Shakespeares	5	2559	298	68	6
Jelly Babies	2	3477	233	422	47
Stargazers	3	3305	143	193	16
Little Britains	5	3656	187	74	21
Giraffe	1	1507	127	60	7

2.4.1 Body mass change

There was no significant correlation between the change in subordinate adult body mass from before to after pup emergence and adult feeding rate to pups (Pearson product-moment correlation: $r = 0.103$, $n = 50$, $p = 0.479$; Figure 2.2A). There was also no significant correlation between subordinate adult body mass change and either pup-grooming duration ($r = -0.080$, $n = 50$, $p = 0.563$; Figure 2.2B) or pup grooming frequency ($r = 0.088$, $n = 50$, $p = 0.521$; Figure 2.2C).

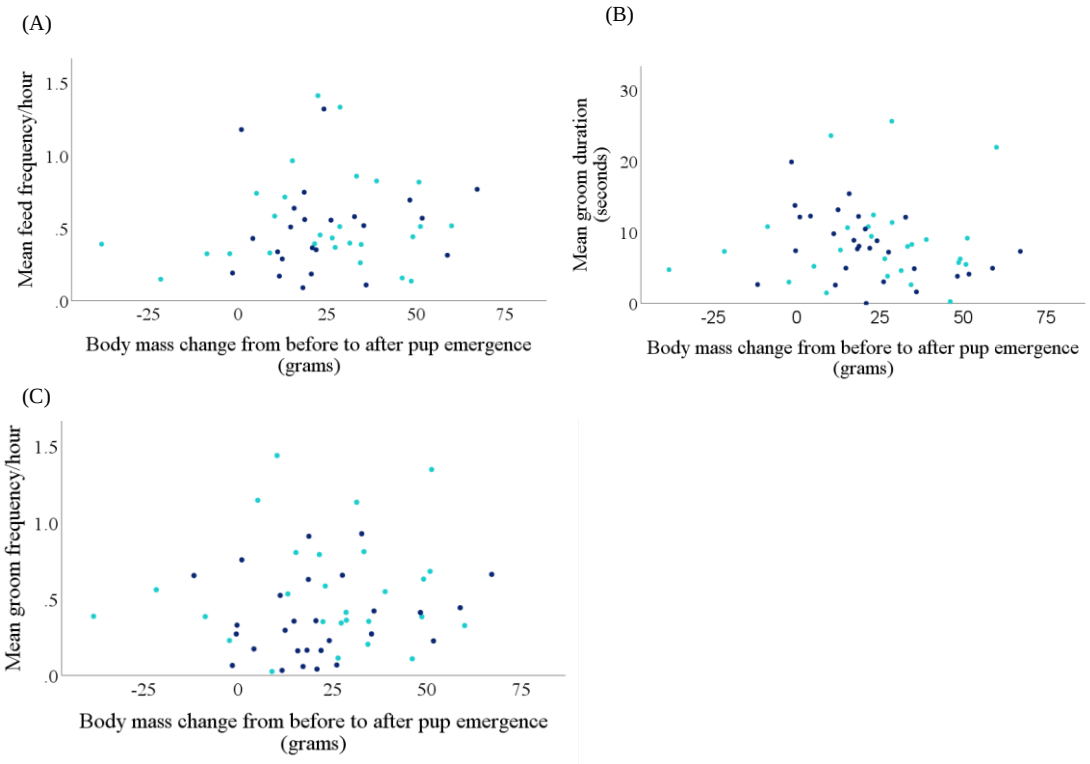

Figure 2.2 Relationship between the change in subordinate adult body mass from before to after pup emergence and (A) mean feed frequency to the pups (B) mean grooming duration of pups, and (C) mean grooming frequency of pups. All figure panels had the same sample size (*n* = 50 adults, 7 groups). Light blue dots = females; dark blue dots = males.

2.4.2 Feeding

The mean feed frequency of all adults was 0.40 ± 0.31 feeds per hour and average food size fed to pups from all adults was 1.75 ± 0.43 from all observed groups (corresponds to the size categories described in the Methods). Dominance status, but not sex, significantly affected pup-feeding frequency when considering all adults (Table 2.2A): subordinate adults fed pups at a higher frequency compared to dominants (Figure 2.3A). Furthermore, subordinate age significantly affected pup-feeding frequency (Table 2.2B): individuals younger than 2 years fed pups at a higher frequency compared to those older than 2 years (Figure 2.3B). Adult dominance status, but not sex, also significantly affected the mean size of food items fed to pups when considering all adults (Table 2.2C): dominants fed larger items than subordinates (Figure 2.3C). Neither age nor sex of subordinates significantly influenced the mean size of food items provided to pups (Table 2.2D, Figure 2.3D).

Table 2.2 Output from GLMMs assessing how dominance status, sex and age of adults affects (A, B) mean pup-feeding frequency and (C, D) mean prey size delivered to pups. Significant fixed terms are highlighted in bold.

GLMM	Fixed effect	Estimate ± SE	df	x^2	*p*	link
(A) Mean feed frequency of all adults						log
Random terms	*Group ID*	0.074 ± 0.271				
Minimal model	(intercept)	-1.843 ± 0.219				
	Dominance	**1.033 ± 0.219**	**1**	**<0.001**	**<0.001**	
Dropped terms	Sex:Dominance		1	0.392	0.393	
	Sex		1	0.674	0.674	
(B) Mean feed frequency of subordinate adults						inverse
Random terms	*Group*	0.022 ± 0.149				
Minimal model	(intercept)	3.006 ± 0.426				
	Age	**-1.278 ± 0.452**	**1**	**0.003**	**0.005**	
Dropped terms	Sex:Age		1	0.750	0.751	
	Sex		1	0.670	0.669	
(C) Mean food size provided by all adults						log
Random terms	*Group ID*	0.006 ± 0.077				
Minimal model	(intercept)	0.685 ± 0.071				
	Dominance	**-0.136 ± 0.057**	**1**	**0.018**	**0.018**	
Dropped terms	Sex:Dominance		1	0.266	0.264	
	Sex		1	0.839	0.839	
(D) Mean food size provided by subordinate adults						
Random terms	*Group*	0.018 ± 0.133				identity
Minimal model	**(intercept)**	**1.812 ± 0.113**			**<0.001**	
Dropped terms	Sex:Age		1	0.950	0.950	
	Sex		1	0.926	0.926	
	Age		1	0.912	0.911	

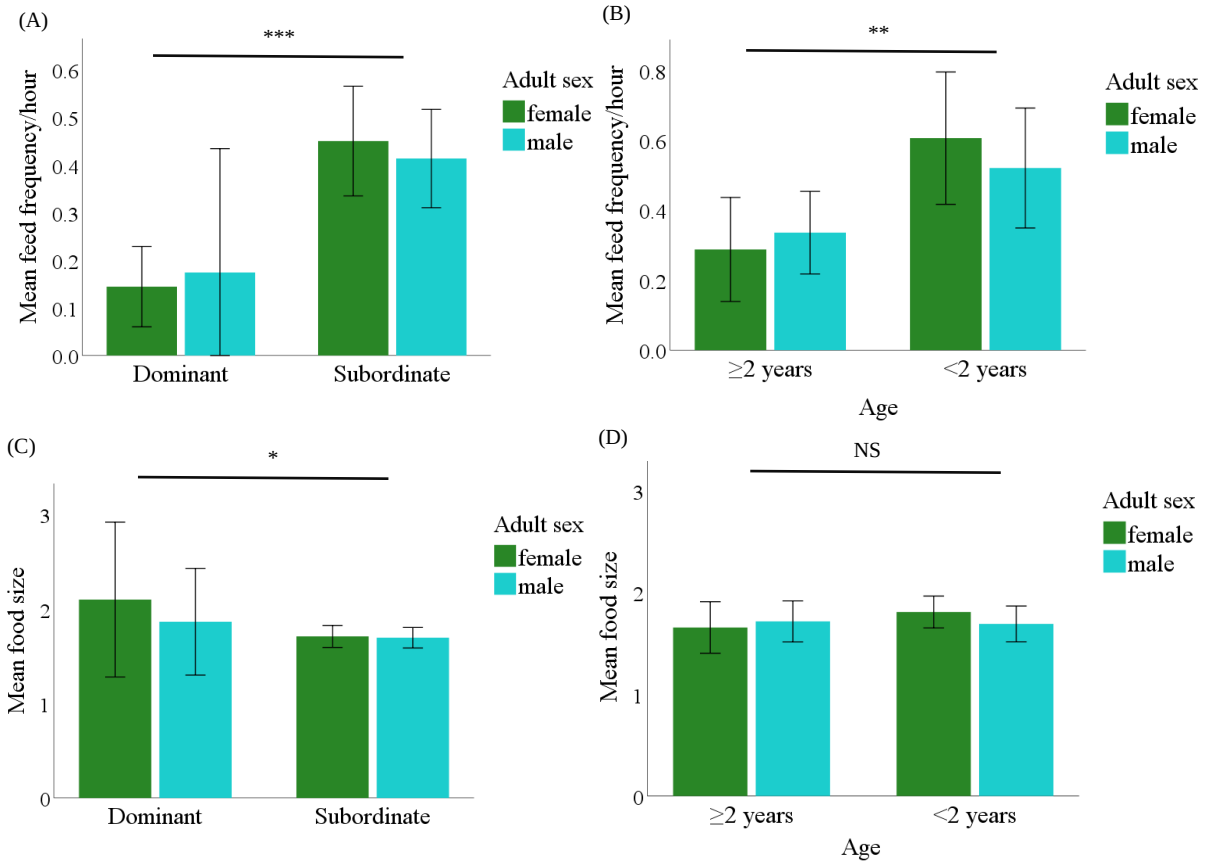

Figure 2.3 Mean ± SD (A, B) frequency of pup feeds and (C, D) size of prey items delivered to pups by adults of different dominance status, sex and age. Food items were categorised into four sizes: small = 1, medium = 2, large = 3, extra-large = 4. Figure panels A and C had the same sample size (n = 80 adults, 7 groups), figure panel B and D had the same sample size (n = 53 adults, 7 groups). NS = nonsignificant. *$p < 0.05$.

2.4.3 Grooming

Mean groom duration by all adults was 7.3 ± 5.3 s and mean groom frequency by all adults was 0.36 ± 0.31 per hour from all observed groups. Pup-grooming frequency was significantly affected by the interaction between dominance status and sex when considering all adults (Table 2.3A). Subordinate females groomed pups at a significantly higher frequency compared to dominant females (Mann-Whitney U test: $U = 56$, $n = 42$, $p = 0.025$; Figure 2.4A), however there was no significant difference between dominant and subordinate males ($U = 95$, $n = 38$, $p = 0.968$; Figure 2.4A). Moreover, sex, but not age, of subordinates significantly affected pup-grooming frequency (Table 2.3B): subordinate females groomed pups at a higher frequency compared to subordinate males (Figure 2.4B). Mean groom duration was significantly affected by dominance status, but not sex, when considering all adults (Table 2.3C): subordinates groomed pups for a longer duration compared to dominants. There was no significant effect of either subordinate age or sex on mean groom duration (Table 2.3D).

Table 2.3 Output for GLMMs assessing how dominance status, sex and age of adults affects (A, B) mean groom frequency and (C, D) mean groom duration. Significant fixed terms are highlighted in bold.

GLMM	Fixed effect	Estimate ± SE	df	x^2	*P*	link
(A) Mean groom frequency per hour by all adults						log
Random terms	*Group*	0.075 ± 0.273				
Minimal model	(intercept)	-1.830 ± 0.329				
	Sex:Dominance	**0.970 ± 0.336**	**1**	**0.333**	**0.031**	
	Dominance	-1.045 ± 0.485			0.004	
	Sex	0.551 ± 0.451			0.222	
(B) Mean groom frequency per hour by subordinate adults						log
Random terms	*Group*	0.052 ± 0.227				
Minimal model	(intercept)	-0.786 ± 0.198				
	Sex	**-0.430 ± 0.211**	**1**	**0.046**	**0.041**	
Dropped terms	Sex:Age		1	0.762	0.762	
	Age		1	0.831	0.832	
(C) Mean groom duration by all adults						identity
Random terms	*Group*	3.035 ± 1.742				
Minimal model	(intercept)	5.521 ± 1.323				
	Dominance	**2.266 ± 1.081**	**1**	**0.099**	**0.036**	
Dropped terms	Sex:Dominance		1	0.089	0.113	
	Sex		1	0.504	0.514	
(D) Mean groom duration by subordinate adults						inverse
Random terms	*Group*	0.001 ± 0.027				
Minimal model	**(intercept)**	**0.110 ± 0.027**			**<0.001**	
Dropped terms	Sex:Age		1	0.987	0.987	
	Sex		1	0.581	0.735	
	Age		1	0.552	0.662	

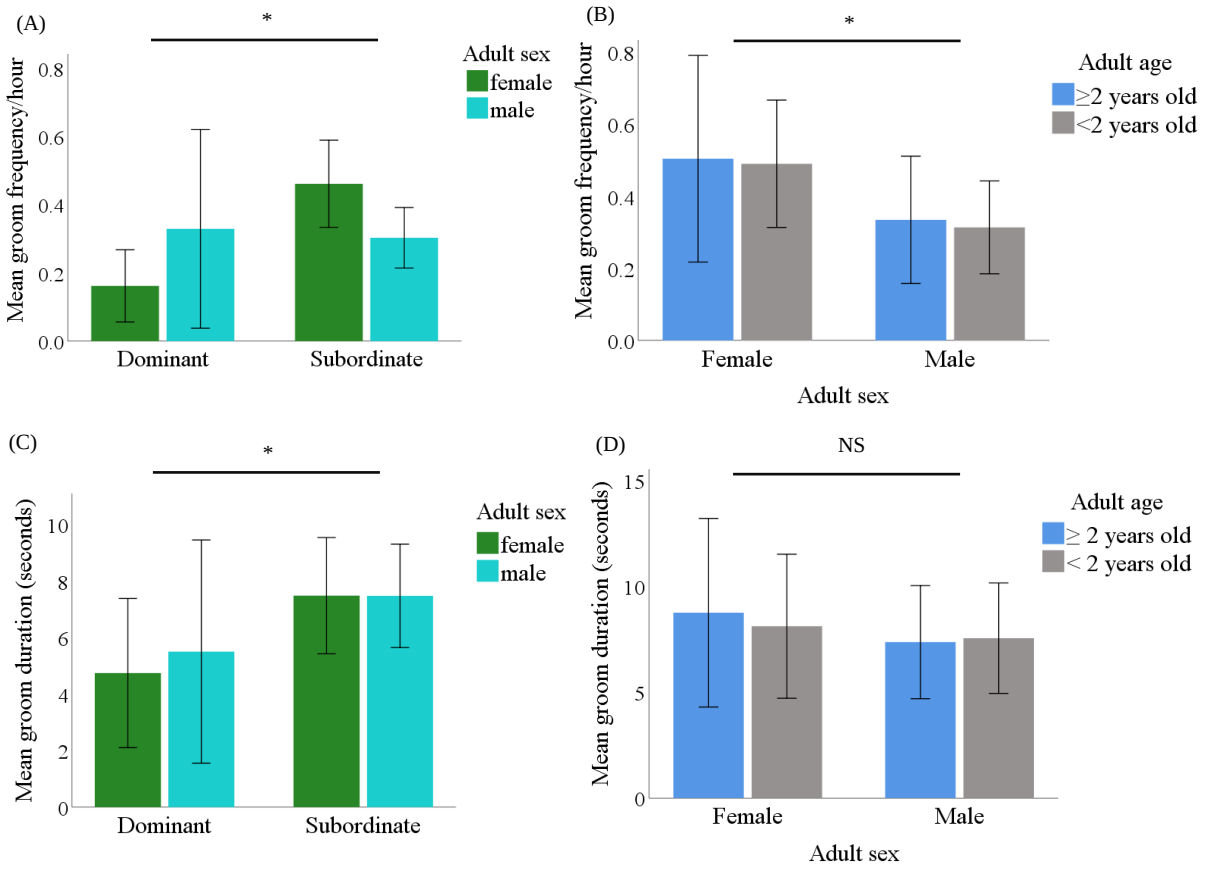

Figure 2.4 Mean ± SD (A, B) groom frequency and (C, D) groom duration by adults of different dominance status, sex and age. Figure panel A and C had same sample size (n = 81, 7 groups), figure panel B and D had the same sample size (n = 54, 7 groups). NS = nonsignificant. *p < 0.05.

2.4.4 Adult sex & pup sex

There was no significant difference in mean feed frequency between subordinate male and female adults to male and female pups (Table 2.4A, Figure 2.5A). There was also no significant difference in mean groom duration between subordinate male and female adults to male and female pups (Table 2.4B, Figure 2.5B).

Table 2.4 LMM output of mean feed frequency per hour by sex of adults and pups of subordinates (A). GLMM output of mean groom duration by sex of adults and pups of subordinates (B).

LMM	Fixed effect	Estimate ± SE	df	x²	*p*	
(A) Mean feed frequency of subordinate adults						
Random terms	*Group*	0.039 ± 0.198				
	adult ID in Group	0.001 ± 0.029				
Minimal model	**(intercept)**	**0.189 ± 0.025**			**<0.001**	
Dropped terms	Adult sex:Pup sex		1	NA	0.066	
	Pup sex		1	NA	0.717	
GLMM	Fixed effect	Estimate ± SE	df	x²	*p*	link
(B) Mean groom duration of subordinate adults						inverse
Random terms	*Group*	0.000 ± 0.000				
	adult ID in Group	0.000 ± 0.000				
Minimal model	**(intercept)**	**0.011 ± 0.002**			**<0.001**	
Dropped terms	Adult sex:Pup sex		1	0.827	0.827	
	Pup sex		1	0.488	0.487	
	Adult sex		1	NA	0.128	

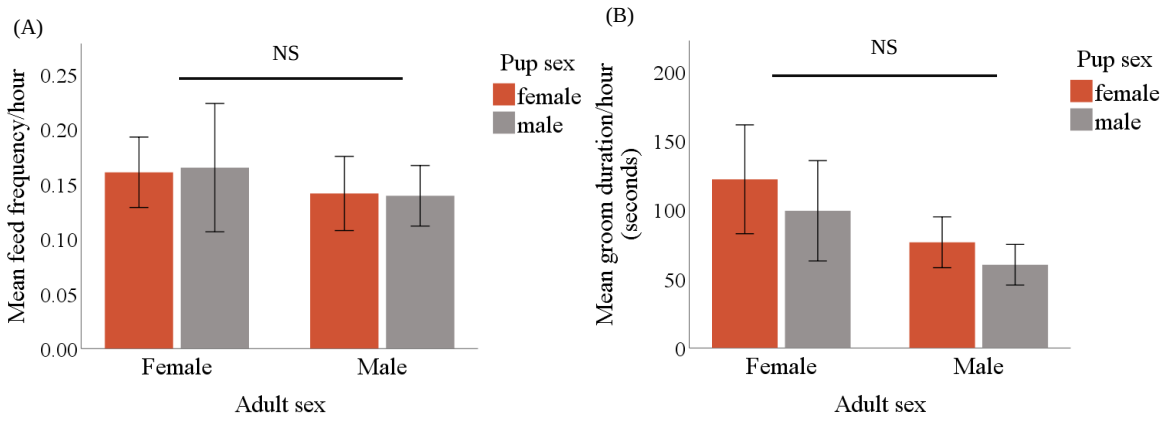

Figure 2.5 Mean ± SD (A) feed frequency and (B) groom duration of male and female subordinates to male and female pups. NS = nonsignificant.

2.4.5 Group-sleeping

The mean group-sleep duration of adults which were observed to sleep with the pups was 574 ± 441 s. The mean number of group sleeping observations of all adults was 2.49 ± 2.75. Dominance status and sex did not significantly affect group-sleeping duration when considering all adults (Table 2.5A). There was also no significant effect of subordinate age or sex on group-sleeping duration (Table 2.5B).

Table 2.5 Output for GLMMs assessing how dominance status and sex affect mean group sleep duration of all adults (A) and how age and sex affect mean group sleep duration of subordinate adults (B). Significant terms are highlighted in bold.

GLMM	Fixed effect	Estimate ± SE	df	x^2	*P*	link
(A) Mean group sleep duration of all adults						log
Random terms	*Group*	0.067 ± 0.259				
Minimal model	**(intercept)**	**6.164 ± 0.199**			**<0.001**	
Dropped terms	Sex:Dominance		1	0.709	0.709	
	Sex		1	0.604	0.605	
	Dominance		1	0.462	0.464	
(B) Mean group sleep duration of subordinate adults						log
Random terms	*Group*	0.079 ± 0.282				
Minimal model	**(intercept)**	**6.147 ± 0.226**			**<0.001**	
Dropped terms	Sex:Age		1	0.632	0.631	
	Sex		1	0.717	0.717	
	Age		1	NA	0.090	

2.4.6 Pilot experiment

There was no significant difference in the time before the first response of subordinate adults to each pup's begging call (Mann-Whitney U test: U = 42, p = 0.842, Figure 2.6A). Moreover, there was no significant difference between male and female subordinates in their latency to respond (U = 37, p = 0.6) as well as between subordinate individuals ≥2 years old and <2 years old in their latency to respond

(U = 36.5, p = 0.545). Although the small sample size of dominant individuals did not allow for analysis between dominance status in response latency, we found the dominant female (F012) responded more than all other group members to the pup begging tracks (Figure 2.6B).

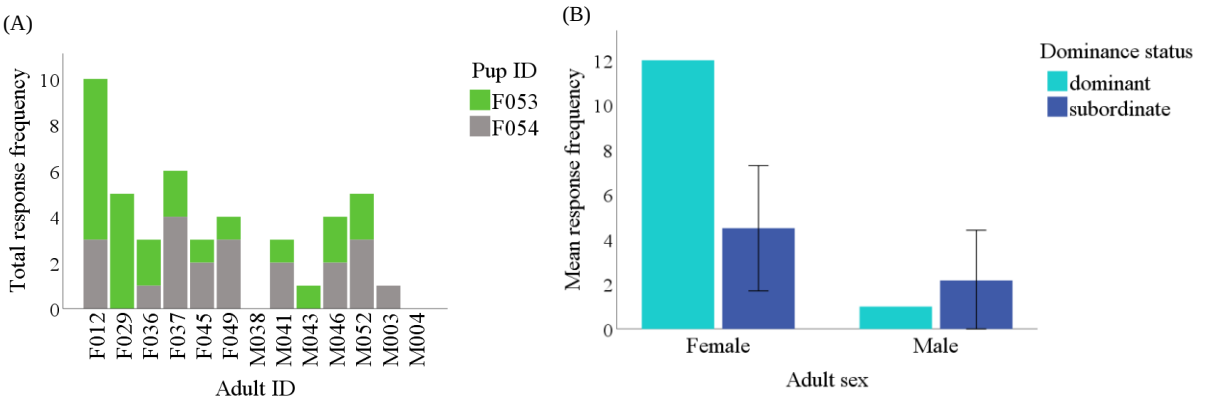

Figure 2.6 Total frequency of each group members response to each pup's begging track (A). F012 and M003 are the dominant individuals. Individuals with their ID beginning with F are female, and M are male. Mean ± SD response frequency to the pup begging track between males and females of dominant and subordinate adults (B).

2.5 Discussion

The results from the adult–pup interactions show differences between group members in the various caring activities. Contrary to predictions, body condition of helpers did not affect feeding investment from helpers. We found that dominance status and age significantly affected feeding frequency, whereas dominance status and sex significantly affected grooming frequency, dominance status significantly affected grooming duration, and there was no significant variation between dominance status, age and sex in group-sleeping bouts. This is the first study to analyse helper variation in alloparental investment between different caring behaviours in dwarf mongooses, adding to the growing literature on intraspecific variation in social mammals.

2.5.1 Feeding

Dominant individuals contributed significantly less than subordinates to feeding the pups, in terms of feeding frequency, which has also been found in meerkats and banded mongooses (Clutton-Brock *et al*. 2004; Gilchrist & Russell 2007). Dwarf mongooses give birth to two to three litters consecutively within a four-month period, so dominants might be reducing their feed frequency to the current litter to increase their energy reserves to produce the next. Hence, the cost which subordinates face by feeding pups is expected to be lower because the probability of reproducing is significantly less (Rood 1980). However, dominants fed pups significantly larger prey items compared to subordinates, which may compensate to some extent for the lower feeding frequency. It has been observed in many social species that dominant individuals will have access to larger prey items (Hamilton & Busse 1982; Murray *et al*. 2006; Flower 2008) and a study by Malcolm & Marten (1982) on wild dog (*Lycaon pictus)* alloparental care found that dominants were more likely than younger pack members to feed pups large prey items. This could be due to having more hunting experience and first access to kills, therefore suffering a reduced cost by feeding pups larger prey items. The similar results found from our study suggests dominant dwarf mongooses could be more efficient foragers and hence able to feed pups larger, higher-quality prey items, although this would need the collection of detailed adult foraging data to test explicitly.

There was no significant difference between males and females in their contribution to feeding activities, either in terms of feeding frequency or the size of prey items provided. This is in contrast to other studies on obligate cooperatively breeding mammals: in meerkats, females helpers gave more food than males (Clutton-Brock *et al*. 2001), which has also been found in brown hyenas (*Hyaena brunnea*) (Owens & Owens 1984) and golden headed lion tamarins (*Leontopithecus chrysomelas*) (Moura *et al*. 2010). Because male dwarf mongooses are more likely than females to emigrate (Rood 1987; Creel & Rabenold 1994), we hypothesised that females would contribute more to feeding pups because they would gain more future benefits, which has been observed in meerkats (Brotherton *et al.* 2001). This was not found from our results, suggesting that there may not be disparities between the sexes in the benefits gained from feeding pups.

We found that younger subordinate helpers (those <2 years old) fed the pups at a significantly higher frequency than older subordinates (those ≥2 years old). This is in-line with a previous study on Damaraland mole-rats, which found that caring effort by non-breeders decreased with age (Zöttl *et al.* 2018). Whereas the opposite result was found in wild dogs when there were food shortages; individuals >2 years old fed pups more than individuals <2 years old (Malcolm & Marten 1982). The age effect in dwarf mongooses could be explained by kin selection as younger individuals are more likely to be siblings of the newborn litter because the dominants are likely to have maintained their dominance role for at least one to two years; younger subordinates might therefore gain greater indirect fitness benefits by assisting the development of pup growth. To determine if kin selection could be acting on variation in feed frequency, genetic analysis of group members and the pups is needed; this is ongoing for the study population, but the results are not yet available.

2.5.2 Grooming

Of all group members, dominant females groomed pups at the lowest frequency, while subordinate females groomed pups at the highest frequency. One explanation for this variation is the differences in cost of grooming between group members. Most grooming attempts by the dominant female would cause the pups to attempt suckling (Emily Grout personal observation), which has a high energetic cost for mothers (Fuchs 1981). Therefore, to reduce this cost, dominant females may reduce the frequency that they groomed the pups.

In contrast to the feeding results, subordinate females groomed pups more than did subordinate males. Grooming serves a social function in many species (Dunbar 1991), including dwarf mongooses (Kern & Radford 2016). Since grooming does not have a direct impact on immediate pup survival, it could be assumed that individuals taking part in grooming interactions are attempting to develop long-term social bonds (Kern & Radford 2016, 2018). As well as increasing social bond strength, in many social mammals, grooming and has been found to increase likelihood of long-term coalitionary support (Seyfarth & Cheney 1984; Kern & Radford 2016). Hence, unlike the results found from the feeding observations, grooming could result in future social benefits for the helpers. As dwarf mongoose males

are more likely than females to emigrate (Rood 1987; Creel & Rabenold 1994), they have a smaller benefit by developing social bonds with the pups compared to females who are more likely to remain in their natal group.

2.5.3 Sex preferences

There was no significant difference between frequency of male and female helpers in grooming duration and feed frequency to male and female pups. Contrasting the findings by Brotherton *et al*. (2001) on meerkat food allocation, there was no significant difference in feed frequency to male and female pups from female helpers. But, the results from Brotherton *et al*. found male helpers fed female and male pups equally which is in-line with our findings. This lack of preference to feed a particular pup suggests adults could be adopting the 'feed the nearest pup' rule which has been found in banded mongooses (Gilchrist 2004). However, banded mongooses also show clear assortment by sex in caring effort by helpers; females tending to female pups and males tending to male pups (Vitikainen *et al*. 2017) which has not been seen in this study on dwarf mongooses.

2.5.4 Group-sleeping

We found no significant difference between sex and dominance status of helpers in group-sleep durations, however there was a non-significant difference between subordinate individuals who were ≥2 years old and individuals <2 years old in average group-sleep duration. Older individuals slept with pups on average for a longer duration. Interestingly the opposite result is seen in the feeding observations. There is large standard deviation in subordinate males ≥2 years old in group sleep duration, suggesting that other factors other than age are causing variation in group-sleeping interactions, such factors could include level of relatedness to pups, individual foraging success, position in the dominance hierarchy and probability of emigrating.

2.5.5 Pilot experiment

We found no significant differences between subordinate adults in their latency to respond to the playback begging calls. However, figure 2.6B illustrates that the dominant female responded more to both speakers compared to other group members. Figure 2.6A demonstrates that there was a large amount of variation between adults in the total number of responses to both pups, with some individuals responding to one pup more than the other (e.g. the highest ranking subordinate female (F029) only responded to one pup (F053), whereas a younger subordinate female (F049) responded more frequently to the other pup (F054)). This suggests that individuals were able to recognise pups based on their vocalisations, however more trials should be run within the same group as well as repeated in multiple groups to determine whether pup recognition through vocalisations does occur.

2.5.6 Conclusion

To summarise, we have found clear differences between adult helpers in their alloparental contributions which differ between tasks. Dominance status and age influenced feeding frequency, whereas dominance status, but not sex or age influenced food size of prey items given to pups. Grooming interactions were affected by sex and dominance of helpers, but not age. There was no clear assortment in grooming interactions between subordinate adult sex and pup sex and there was no significant difference between all group members in group sleeping bouts. Furthermore, the pilot study found no sex or age differences between subordinates in response latency to the pup begging tracks, however this experiment had a limited sample size and was conducted under time constraints, therefore future studies should repeat the experiment to multiple groups to determine if patterns in response latency to different pups between group members emerge. Our findings have added to the growing body of research on intraspecific variation in alloparental activities. These results demonstrate that the costs and benefits associated with the different caring activities vary depending on the task and future studies examining variation in alloparental investment should analyse multiple caring activities to gain a greater understanding of the factors which could be causing this variation.

Chapter 3: General Discussion

3.1 Summary of findings

This study has found significant differences in adult investments in pup-rearing activities in dwarf mongooses (*Helogale parvula*). We found subordinate individuals who were younger than 2 years old fed pups at a significantly higher rate compared to subordinates who were 2 years and older, as was previously found by Rood (1978), however adult sex did not influence feeding frequency which does not agree with previous findings (Rasa 1977; Rood 1978). Contrary to this, the sex of adults, rather than age, influenced pup-grooming frequency; subordinate females groomed pups at a significantly higher frequency compared to males and subordinate individuals groomed pups for a significantly longer duration compared to dominants. We found no observable difference between groom duration and feed frequency by male and female adults to male and female pups. Furthermore, there was no significant difference between adults in time spent group-sleeping with the pups, however older individuals had longer average group-sleep durations. In conclusion, there was clear variation in caring investment depending on the helping task which suggests that there are differing costs and benefits of each behaviour between individuals. Particular behaviours (such as grooming) could have long-term benefits by developing social bonds (Kern & Radford 2016), and therefore may be more frequently conducted by group members who are more likely to stay in the group.

Our results do not corroborate with the findings from previous alloparental studies in dwarf mongooses as well as in closely related species (Rasa 1977; Rood 1978; Brotherton *et al*. 2001; Clutton-Brock *et al*. 2001; Vitikainen *et al*. 2017). Previous studies on meerkats (*Suricata suricatta*) found that the foraging efficiency of helpers influence pup feeding rates (Clutton-Brock *et al*. 2000), which we did not find in this study. Sex of meerkat helpers has been found to affect pup feeding rates (Brotherton *et al.* 2001), which we did not observe in dwarf mongooses. Furthermore, banded mongooses (*Mungos mungo*) demonstrate clear sex assortment in caring activities, with males caring for male pups and females caring for female pups (Vitikainen *et al*. 2017), which we did not find in this study. This illustrates that there is variation in alloparental investment between individuals in closely related species.

3.2 Limitations

Dwarf mongooses are an excellent study species to examine alloparental behaviours because habituation can allow close observational data collection in natural conditions as well as field-based experimental manipulations (Kern & Radford 2013). However, when a female gives birth, the pups remain underground for approximately 12 days; during this time, it is assumed that they are being groomed by the babysitter, sleep in groups and are being fed milk by the dominant female (and potentially subordinate females). Little is actually known about the alloparental behaviours exhibited during this period despite it being an important stage in pup development. Therefore, to allow examination into the various alloparental behaviours exhibited before the pups emerge from the sleeping burrow, an infrared video-recording device could be inserted into the burrow to collect observational data on the interactions which occur between the adults and pups. Recorded behaviour could be compared to the investment in helping efforts when the pups emerge from the sleeping burrow to determine whether particular individuals change their level of investment in pup care before and after pup emergence. The risk from inserting a camera into the sleeping burrow is that individuals could perceive the novel object as a predator and as a result change their behaviour, potentially moving the pups prematurely to a different burrow.

This study was conducted on just the first litter of pups in the 2018–2019 breeding season. Collecting data over multiple litters from the same breeding season as well as over several breeding seasons would increase the sample size and allow comparative analysis of variation in caring investments between litters. Ten days after the pups from the first litter of the breeding season emerged, the dominant pair in at least some groups was observed mating, which suggests their investment in pup care would be reduced to build up enough energy reserves to undergo gestation of a second litter. Therefore, it could be hypothesised that dominant individuals would invest more in caring activities for the final litter of pups born in the breeding season. Hence, comparative analysis between generations would allow greater understanding of the factors contributing to pup care.

Due to limited time and resources, DNA analysis was not feasible for this study. Future research would benefit from understanding the level of relatedness between helpers and pups to determine

whether group members are maximising their inclusive fitness by preferentially caring for close relatives. Other studies have found conflicting results from relatedness data and its importance in determining variation in alloparental behaviours. Phylogenetic analysis comparing across species, conducted by Briga *et al*. (2012), found a positive correlation between relatedness and allomaternal care; species living in groups with high levels of relatedness are more likely to exhibit allomaternal care. However, in cooperatively breeding meerkats and banded mongooses, relatedness has not been found to affect variation in alloparental care (Clutton-Brock *et al*. 2001; Vitikainen, *et al.* 2017).

3.3 Potential future studies

The pilot experimental study found no significant differences between the sex and age of adults who responded to the speakers as well as between the pup begging calls. Clearly a larger sample size is required, in terms of both adults and groups tested; to improve this experiment further, repeated testing could occur over multiple generations. Due to time constraints and limited sample size, different response types (such as looking, approaching and sniffing the speaker) were not included in the analysis, however analysis of these various responses between group members could be done in the future with a larger sample size.

There are a variety of directions future experiments could take to examine adult responses to pup begging calls. First, comparing responses to playback of male and female begging calls (whilst also conducting acoustic analyses to determine if there are indicators of sex in the calls alone) would determine whether adults exhibit biased sex assortment as found in banded mongooses (Vitikainen *et al*. 2017). Furthermore, adult responses to playbacks of same-sex individuals begging at different rates could be conducted to determine whether adults respond differently depending on the pup's hunger state; this could be coupled with supplementary feeding experiments to test the relationship between pup state and begging rate. As found in banded mongooses by Bell (2007), the number of pups in a group can affect the begging rate per individual, which in turn can influence the rate at which they are fed. To determine if this is seen in dwarf mongooses, a playback experiment which manipulates the vocal density of pups present in the group would develop our understanding of adult responsiveness to

differing litter sizes. Finally, repeating the experiments as the pups get older would allow consideration of whether adults change their level of response as the pups develop. To summarise, this is a relatively unexplored field of research in variation in adult responsiveness. As found from the pilot playback study, dwarf mongooses are a good system to conduct experiments to answer questions regarding variation in alloparental investment.

To analyse whether the state of the helpers and the pups influence variation in alloparental activities, supplementary feeding experiments could be conducted with both the adults and the pups. A focal adult could be given supplementary food and then their interactions with the pups would be observed. It could be hypothesised that a high-quality individual (who was given the additional food) would invest more in pup-care activities because they do not need to forage and therefore would optimise their inclusive fitness. Moreover, if a pup was supplementary fed, it could be hypothesised that this individual would reduce their begging frequency and as a result would be fed a reduced amount from the adults. Since this population is habituated, it is possible to control which individual is being fed, making it an excellent study system to conduct this type of experiment. In unhabituated populations, it will be challenging to control for other group members eating the additional food given, therefore a trapping device where the focal individual could be held to eat the supplementary meal could be used, but this may distress the focal individual and subsequently affect their following behaviour when released. Therefore, in unhabituated populations, this type of experiment needs to consider these conflicting issues to ensure accurate results.

Clutton-Brock *et al*. (1998) found that meerkat adults in smaller groups babysat more frequently. To determine if group size does affect the level of helping behaviour in dwarf mongooses, playback experiments could be conducted to affect the perceived number of individuals in the group. For example, additional pup calls could be played near the pups to mimic a greater number of pups in the group. Comparative analysis of the helping investment before, during and after the playback would determine whether adults adjust their helping efforts accordingly to pup demand. This playback experiment could also be run to mimic additional adult helpers by playing back the feed call adults use when they have caught a food item to give to a pup. This is a less invasive experiment than changing

the actual group size by removing or adding individuals in the group as this is likely to disrupt multiple aspects of group living and conclusions made would need to consider these impacts carefully.

This study has focused on the adults involved in pup-caring activities. However, future research could also examine the pup interactions with the adults. A social network was built to illustrate the differences between adult to pup and pup to adult grooming interactions (Figure 3.1). Pups were observed to groom fewer adults whereas the majority of adults were observed to groom all the pups. The social network illustrates that the dominant male was groomed for a longer average duration by two of the three pups compared to all other group members. This could suggest that pups are able to distinguish dominance at an early age, but clearly larger sample sizes and an experimental study are needed for strong conclusions.

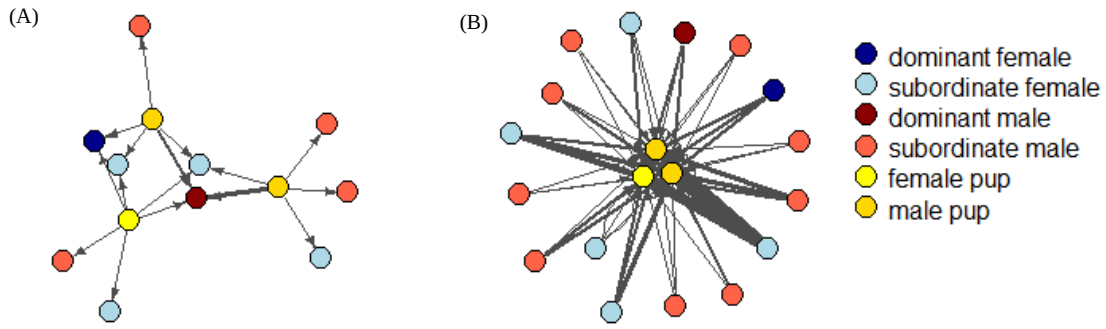

Figure 3.1 Social network illustration of pup to adult grooming interactions (A) and adult to pup grooming interactions (B) in the dwarf mongoose group named Bookworms. Social networks were constructed in RStudio 3.5.2 (R Development Core Team 2018) using the igraph package to visualise the network (Csardi & Nepusz 2006). Each node represents one group member (sex and dominance coded by colour as shown in the key). Arrow denotes direction of the grooming interaction. Thickness of arrow stem represents the sum of the grooms observed over the total observation period with the group in this study. Force-directed layout was chosen to ensure no edges crossed over in the visualisation.

3.4 Additional observational data

The majority of adult–pup interactions were feeding, grooming and group-sleeping, however other behaviours were observed during the observation period which were not included in this study due to time constraints and limited sample sizes for statistical analysis. These behaviours include babysitting, suckling, moving pups, play and aggressive interactions.

Babysitting is an energetically costly task for helpers (Clutton-Brock *et al*. 1998), so there is likely variation between group members in babysitting investment. This will shed light onto various factors which could be determining variation in alloparental investment such as group size, age, sex and weight of helpers as found in meerkats by Clutton-Brock *et al*. (1998, 2000) and breeding status and time of day as found in banded mongooses by Cant (2003).

Allosuckling has been observed in many cooperatively breeding mammals, but it is an energetically costly behaviour, and therefore it is not expected for subordinates to provide milk for non-offspring (König 2006). However, allosuckling is common in dwarf mongooses; the adaptive benefit for this behaviour is under debate (Jennions & Macdonald 1994; Keane *et al.* 1994). The dominant female does not reproductively suppress subordinate females (Creel & Waser 1991), which could suggest that the dominant female benefits from subordinate female reproduction. Previous genetic analysis on dwarf mongooses by Keane *et al.* (1994) found that the direct fitness that a subordinate would gain by reproducing was lower compared to the indirect fitness gained by helping raise non-offspring, because dwarf mongooses have high within-group relatedness (Rasa 1989). One hypothesis for allowing subordinate reproduction is that it will increase the group size, which has been found to significantly influence pup survival (Creel & Creel 1991). Therefore, to determine whether group size is a significant indicator for variation in allosuckling investment, observational data should be collected on all suckling bouts by the dominant and subordinate females between different group sizes.

When pups begin to emerge from the sleeping burrow, between 10 and 14 days after birth, their ability to move with the group is limited. Hence, group members assist with the moving of pups between sleeping burrows as well as to sheltered areas throughout the day; to avoid detection from predators. The moving of pups is vital for pup survival when they lack the physical ability to move independently

with the group, however this can be a costly task (Sánchez *et al.* 1999). To date, there has been no study which has analysed variation between individuals involved in moving pups in cooperatively breeding mammals, with most studies classifying pup moving as a form of babysitting (Courchamp *et al.* 2002; Gilchrist 2004). Our results have demonstrated that adults vary in their contribution to different alloparental tasks. Therefore, to develop our understanding on variation in alloparental behaviours, analysis of the individuals involved in control of the position of the pups within the group and their movement between sleeping burrows should be considered in future studies.

Play has been well studied in cooperatively breeding mammals and is thought to serve multiple benefits to the development of young (Graham & Burghardt 2010). Previous studies on meerkats has found that play does not serve any social cohesion benefits (Sharpe 2005). However, no research has been conducted on the individuals involved in play in dwarf mongooses. When pups become more independent from helpers and begin foraging for their own food, they become more active in play interactions with older group members as well as between each other. Future research could examine the play interactions between pups and helpers to determine whether it serves an evolutionary benefit such as increasing speed of pup development or social cohesion as well as determining whether it should be categorised as a form of alloparental care if additional benefits are found.

All interactions in this study analysed positive behaviours which benefits pup survival and social development. However, not all individuals were positively caring for the pups, with some individuals observed to steal food items from the pups as well as pushing pups out of burrowed holes containing a rich food source to forage for themselves (Emily Grout personal observation). These antagonistic interactions should be documented in future studies to investigate the evolutionary benefit of aggressive behaviours.

3.5 Conclusion

Alloparental care has been widely studied although the variation between group members in their caring efforts has been limited to few species. Here, we provide the first study on variation in alloparental tasks in cooperatively breeding dwarf mongooses. This variation between helping tasks demonstrates that to

have a better understanding in alloparental behaviour, all interactions should be recorded. Adults could be partitioning their caring efforts depending on the short and long term costs and benefits that each behaviour involves. These costs and benefits are likely to vary between group members depending on certain factors including; likelihood of emigrating, social and dominance status as well as their foraging efficiency and individual quality. In conclusion, this study has demonstrated that there is variation in alloparental tasks between group members, and a combination of observation and experimental manipulation studies should be conducted to determine the factors contributing to such variation.

References

Abbot, P., Abe, J., Alcock, J., Alizon, S., Alpedrinha, J. A., Andersson, M., . . . Barton, N. (2011). Inclusive fitness theory and eusociality. *Nature, 471*(7339), E1.

Ang, T.Z. & Manica, A. (2010). Aggression, segregation and stability in a dominance hierarchy. *Proceedings of the Royal Society B: Biological Sciences, 277*(1686), 1337-1343.

Arroyo, B., Mougeot, F. & Bretagnolle, V. (2001). Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behavioral Ecology and Sociobiology, 50*(2), 109-115.

Arnold, W. (1993). Social evolution in marmots and the adaptive value of joint hibernation. *Verhandlungen der Deutschen Zoologischen Gesellschaft, 86*, 79-94.

Augusto, J. F., Frasier, T. R., & Whitehead, H. (2017). Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. *Marine Mammal Science, 33*(2), 440-456.

Aureli, F., & Yates, K. (2009). Distress prevention by grooming others in crested black macaques. *Biology Letters*, *6*(1), 27-29.

Ausband, D. E., Mitchell, M. S., Bassing, S. B., Nordhagen, M., Smith, D. W., & Stahler, D. R. (2016). Dog days of summer: influences on decision of wolves to move pups. *Journal of Mammalogy, 97*(5), 1282-1287.

Bartholomew, G. A. (1959). Mother-young relations and the maturation of pup behaviour in the Alaska fur seal. *Animal Behaviour, 7*(3-4), 163-171.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv, 1406*(5823).

Beecher, M. D. (1988). Kin recognition in birds. *Behavior Genetics, 18*(4), 465-482.

Beisiegel, B. M. (2001). Notes on the coati, *Nasua nasua* (Carnivora: Procyonidae) in an Atlantic forest area. *Brazilian Journal of Biology, 61*(4), 689-692.

Bell, M (2007). Cooperative begging in banded mongoose pups. *Current Biology,17*(8), 717-721

Bell, M. (2008). Strategic adjustment of begging effort by banded mongoose pups. *Proceedings of the Royal Society B: Biological Sciences, 275*, 1313-1319.

Bergmüller, R., & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by pre-emptive appeasement. *Animal Behaviour, 69*(1), 19-28.

Bergmüller, R., Johnstone, R. A., Russell, A. F., & Bshary, R. (2007). Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes, 76*(2), 61-72.

Birch, J., & Okasha, S. (2015). Kin Selection and Its Critics. *BioScience, 65*(1), 22-32.

Blumstein, D., & Armitage, K. (1999). Cooperative breeding in marmots. *Oikos, 84*(3), 369-382.

Blumstein, D. T. & Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences, 272*(1573), 1663-1668.

Brandl, S. J., & Bellwood, D. R. (2015). Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes. *Scientific Reports, 5*, 14556.

Briga, M., Pen, I., & Wright, J. (2012). Care for kin: within-group relatedness and allomaternal care are positively correlated and conserved throughout the mammalian phylogeny. *Biology Letters, 8*(4), 533-536.

Brotherton, P., Clutton-Brock, T. H., O'Riain, M., Gaynor, D., Sharpe, L., Kansky, R., & McIlrathb, G. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioural Ecology, 12*(5), 590-599.

Brown, J. L. (1987). Helping and communal breeding in birds: ecology and evolution. *Princeton University Press*, 300-301.

Brown, C. R., & Brown, M. B. (1987). Group-living in cliff swallows as an advantage in avoiding predators. *Behavioral Ecology and Sociobiology*, *21*(2), 97-107.

Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male primate society. *Nature, 425*, 179–181.

Burda, H., Honeycutt, R. L., Begall, S., Locker-Grütjen, O. & Scharff, A. (2000). Are naked and common mole-rats eusocial and if so, why?. *Behavioral Ecology and Sociobiology*, *47*(5), 293-303.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences, 106*(33), 13850-13853.

Cant, M. A. (2003). Patterns of helping effort in co-operatively breeding banded mongooses *(Mungos mungo*). *Journal of Zoology, 259*(2), 115-121.

Cant, M. A., Otali, E., & Mwanguhya, F. (2001). Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology, 254*(2), 155-162.

Carter, G., & Leffer, L. (2015). Social Grooming in Bats: Are Vampire Bats Exceptional? *PLoS ONE, 10*(10), e0138430.

Christensen, C., & Radford, A. N. (2018). Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behavioral Ecology, 29*(5), 1004–1013.

Clark, C. W. & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology*, *30*(1), 45-75.

Clutton-Brock, T. H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science, 296*(5565), 69-72.

Clutton-Brock, T. H. (2006). Cooperative breeding in mammals. In *Cooperation in Primates and Humans*, 173-190. Berlin, Heidelberg: Springer.

Clutton-Brock, T. H. (2009). Cooperation between non-kin in animal societies. *Nature, 462*, 51-57.

Clutton-Brock, T. H., Brotherton, P., O'Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R., . . . McIlrath, G. M. (2001). Contributions to cooperative rearing in meerkats. *Animal Behaviour, 61*(4), 705-710.

Clutton-Brock, T. H., Brotherton, P., O'Riain, M., Griffin, A., Gaynor, D., Sharpe, L., . . . McIlrath, G. (2000). Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 267*(1440), 301-305.

Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A., McIlrath, G., Chadwick, P., . . . Skinner, J. D. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society of London. Series B: Biological Sciences, 265*(1392), 185-190.

Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N., Gaynor, D., Kansky, R., Griffin, A. S., & Manser, M. (1999). Selfish sentinels in cooperative mammals. *Science, 284*(5420), 1640-1644.

Clutton-Brock, T. H., Russell, A. F., & Sharpe, L. L. (2003). Meerkat helpers do not specialize in particular activities. *Animal Behaviour, 66*(3), 531-540.

Clutton-Brock, T. H., Russell, A. F., & Sharpe, L. L. (2004). Behavioural tactics of breeders in cooperative meerkats. *Animal Behaviour, 68*(5), 1029-1040.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z., & McIlrath, G. M. (2002). Evolution and development of sex differences in cooperative behavior in meerkats. *Science, 297*(5579), 253-256.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics, 29*(1), 141-177.

Cornwallis, C. K., West, S. A., & Griffin, A. S. (2009). Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. *Journal of Evolutionary Biology, 22*(12), 2445-2457.

Courchamp, F., Grenfell, B., & Clutton-Brock, T. (1999). Population dynamics of obligate cooperators. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1419), 557-563.

Courchamp, F., Rasmussen, G. S., & Macdonald, D. W. (1999). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioural Ecology, 13*(1), 20-27.

Crawley, M. J. (2007). *The R book.* Chichester, UK: Wiley.

Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution, 16*(9), 491-497.

Creel, S. R., & Creel, N. M. (1991). Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology, 28*(4), 263-270.

Creel, S. R., & Rabenold, K. N. (1994). Inclusive fitness and reproductive strategies in dwarf mongooses. *Behavioral Ecology, 5*(3), 339–348.

Creel, S. R., & Waser, P. M. (1991). Failures of reproductive suppression in dwarf mongooses *(Helogale parvula*): accident or adaptation? *Behavioural Ecology, 2*(1), 7-15.

Creel, S., Creel, N. M., Mills, M. G., & Monfort, S. L. (1997). Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behavioral Ecology, 8*(3), 298–306.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, *1695*(5), 1-9.

Denault, L. K., & McFarlane, D. A. (1995). Reciprocal altruism between male vampire bats, *Desmodus rotundus*. *Animal Behaviour, 49*(3), 855-856.

Dunbar, R. I. (1991). Functional significance of social grooming in primates. *Folia Primatologica, 57*(3), 121-131.

Duncan, C., Gaynor, D., & Clutton-Brock, T. (2018). The importance of being beta: female succession in a cooperative breeder. *Animal Behaviour, 146*, 113-122.

East, M., Hofer, H., & Turk, A. (1989). Functions of birth dens in spotted hyaenas (*Crocuta crocuta)*. *Journal of Zoology, 219*(4), 690-697.

Eberle, M., & Kappeler, P. M. (2006). Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioral Ecology and Sociobiology, 60*(4), 582–588.

Emlen, S. T., & Vehrencamp, S. L. (1983). Cooperative breeding strategies among birds. *Perspectives in ornithology*, 93-120.

Evans, J. C., Votier, S. C., & Dall, S. R. (2016). Information use in colonial living. *Biological Reviews, 91*(3), 658.

Evans, K. J., Pavelka, M. S., Hartwell, K. S., & Notman, H. (2012). Do adult male spider monkeys (*Ateles geoffroyi*) preferentially handle male infants? *International Journal of Primatology, 33*(4), 799-808.

Falcón-Cortés, A., Boyer, D., & Ramos-Fernández, G. (2019). Collective learning from individual experiences and information transfer during group foraging. *Journal of The Royal Society Interface, 16*(151), 20180803.

Fedurek, P., Dunbar, R.I. & British Academy Centenary Research Project. (2009). What does mutual grooming tell us about why chimpanzees groom?. *Ethology, 115*(6), 566-575.

Finkenwirth, C., & Burkart, J. M. (2018). Why help? Relationship quality, not strategic grooming predicts infant-care in group-living marmosets. *Physiology & Behavior, 193*, 108-116.

Flower, T. P. (2008). *Competition for food in meerkats (Suricata suricatta).* Doctoral dissertation, University of Pretoria.

Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature, 293*, 466–467.

Freeman-Gallant, C. R. (1996). DNA fingerprinting reveals female preference for male parental care in Savannah sparrows. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 263*(1367), 157-160.

Fuchs, S. (1981). Consequences of premature weaning on the reproduction of mothers and offspring in laboratory mice. *Zeitschrift für Tierpsychologie, 55*(1), 19-32.

Fullerton, C., Berryman, J. C., & Porter, R. H. (1974). On the nature of mother-infant interactions in the guinea-pig (*Cavia porcellus*). *Behaviour*, 145-156.

Gaston, A. J. (1978). The evolution of group territorial behavior and cooperative breeding. *American Naturalist, 112*, 1091–1100.

Gerlach, G. (1996). Emigration mechanisms in feral house mice – a laboratory investigation of the influence of social structure, population density, and aggression. *Behavioral Ecology and Sociobiology, 39*(3), 159-170.

Gerlach, G., & Lysiak, N. (2006). Kin recognition and inbreeding avoidance in zebrafish, *Danio rerio*, is based on phenotype matching. *Animal Behaviour, 71*(6), 1371-1377.

Gero, S., Engelhaupt, D., Rendell, L., & Whitehead, H. (2009). Who Cares? Between-group variation in alloparental caregiving in sperm whales. *Behavioral Ecology, 20*(4), 838-843.

Gilchrist, J. S. (2004). Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behavioral Ecology, 15*(6), 952–960.

Gilchrist, J. S. (2006). Female eviction, abortion, and infanticide in banded mongooses (*Mungos mungo*): implications for social control of reproduction and synchronized parturition. *Behavioral Ecology, 17*(4), 664-669.

Gilchrist, J. S., & Russell, A. F. (2007). Who cares? Individual contributions to pup care by breeders vs non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology, 61*(7), 1053–1060.

Gilchrist, J. S., Otali, E., & Mwanguhya, F. (2004). Why breed communally? Factors affecting fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology, 57*(2), 119-131.

Gilchrist, J., Otali, E., & Mwanguhya, F. (2008). Caregivers recognize and bias response towards individual young in a cooperative breeding mammal, the banded mongoose. *Journal of Zoology, 275*, 41-46.

Gittleman, J. L. (1989). Carnivore Group Living: Comparative Trends. In *Carnivore Behavior, Ecology, and Evolution*, 183-207. Boston, MA: Springer.

Gittleman, J. L., & Thompson, S. D. (1988). Energy Allocation in Mammalian Reproduction. *Integrative and Comparative Biology, 28*(3), 863–875.

Gobush, K., Kerr, B., & Wasser, S. (2009). Genetic relatedness and disrupted social structure in a poached population of African elephants. *Molecular Ecology, 18*(4), 722-734.

Goldizen, A. (1987). Tamarinds and marmosets: communal care of offspring. *Primate Societies*, 4-43.

Gompper, M. E. (1996). Sociality and asociality in white-nosed coatis (*Nasua narica*): Foraging costs and benefits. *Behavioral Ecology, 7*(3), 254-263.

Gompper, M. E., Gittleman, J. L., & Wayne, R. K. (1997). Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica. Animal Behaviour, 53*(4), 781-797.

Graham K. L., & Burghardt, G. M. (2010). Current perspectives on the biological study of play: signs of progress. *The quarterly Review of Biology, 85*(4), 393-418.

Green, J. P., Freckleton, R. P., & Hatchwell, B. J. (2016). Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton's Rule. *Nature Communications, 7*, 12663.

Griffin, A. S., & West, S. A. (2002). Kin selection: fact and fiction. *Trends in Ecology and Evolution, 17*(1), 15-21.

Griffin, A. S., & West, S. A. (2003). Kin Discrimination and the Benefit of Helping in Cooperatively Breeding Vertebrates. *Science, 302*(5645), 634-636.

Gusset, M., & Macdonald, D. W. (2010). Group size effects in cooperatively breeding African wild dogs. *Animal Behaviour, 79*(2), 425-428.

Haldane, J. B. (1955). Population genetics. *New Biology, 18*, 34-51.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology, 7*(1), 1-16.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of theoretical biology, 7*(1), 17-52.

Hamilton, W. J., & Busse, C. (1982). Social dominance and predatory behavior of chacma baboons. *Journal of Human Evolution, 11*(7), 567-573.

Hammerschmidt, K., & Fischer, J. (1998). Maternal discrimination of offspring vocalizations in Barbary macaques (*Macaca sylvanus*). *Primates, 39*(2), 231–236.

Hart, B. L., & Hart, L. A. (1992). Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour, 44*(6), 1073-1083.

Hass, C. C., & Valenzuela, D. (2002). Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). *Behavioral Ecology and Sociobiology, 51*(6), 570-578.

Hatchwell, B. (1999). Investment strategies of breeders in avian cooperative breeding systems. *The American Naturalist, 154*(2), 205-219.

Hayes, L. D. (2000). To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour, 59*(4), 677-688.

He, J., Chen, Q., Wei, Y., Jiang, F., Yang, M., Hao, S., Guo, X., Chen, D. & Kang, L., (2016). MicroRNA-276 promotes egg-hatching synchrony by up-regulating brm in locusts. *Proceedings of the National Academy of Sciences*, *113*(3), 584-589.

Heinsohn, R. (2004). Parental care, load-lightening, and costs. In W. Koenig, & J. Dickinson, *Ecology and Evolution of Cooperative Breeding in Birds*, 67-80.

Herberstein, M. E., & Schneider, J. M. (2018). Advantages of social foraging in crab spiders: Groups capture more and larger prey despite the absence of a web. *Ethology*, *124*(10), 695-705.

Hodge, S. J. (2007). Counting the costs: the evolution of male-biased care in the cooperatively breeding banded mongoose. *Animal Behaviour*, *74*(4), 911-919.

Holekamp, K. E., Ogutu, J. O., Dublin, H. T., Frank, L. G., & Smale, L. (1993). Fission of a spotted hyena clan: consequences of prolonged female absenteeism and causes of female emigration. *Ethology*, *93*(4), 285-299.

Holekamp, K. E., Cooper, S., Katona, C., Berry, N., Frank, L., & Smale, L. (1997). Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy*, *78*, 55-64.

Hudson, R., & Shellman-Reeve, J. (1997). The general protected invasion theory: sex biases in parental and alloparental care. *Evolutionary Ecology*, *11*, 357-370.

Hughes, W. O., Oldroyd, B. P., Beekman, M., & Ratnieks, F. L. (2008). Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science*, *320*(5880), 1213-1216.

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, 215-267.

Jarvis, J. U. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*, *212*(4494), 571-573.

Jennions, M., & Macdonald, D. (1994). Cooperative breeding in mammals. *Trends in Ecology and Evolution*, *9*(3), 89-93.

Jungwirth, A., Josi, D., Walker, J. & Taborsky, M. (2015). Benefits of coloniality: communal defence saves anti-predator effort in cooperative breeders. *Functional Ecology*, *29*(9), 1218-1224.

Kaufmann, J. H. (1962). Ecology and the social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. *University of California publications in Zoology, 60*, 185.

Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliott, L. F., & Minchella, D. J. (1994). Subordinate reproduction in dwarf mongooses. *Animal Behaviour, 47*(1), 65-75.

Kennedy, P., Higginson, A. D., Radford, A. N., & Sumner, S. (2018). Altruism in a volatile world. *Nature, 555*(7696), 359.

Kern, J. M., & Radford, A. N. (2013). Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. *Animal Behaviour, 85*(5), 967-975.

Kern, J. M., & Radford, A. N. (2014) Sentinel dwarf mongooses (*Helogale parvula*) exhibit flexible decision making in relation to predation risk. *Animal Behaviour*, 98, 185-192.

Kern, J. M., & Radford, A. N. (2016) Social-bond strength influences vocally mediated responses to mobbing. *Biology Letters*. 12, 20160648.

Kern, J. M., & Radford, A. N. (2018). Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. *Proceedings of the National Academy of Sciences, USA, 15*, 6255–6260.

Kingma, S. A. (2017). Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. *Nature Communications, 8*(1), 1094.

Kleiman, D. G., & Malcolm, J. R. (1981). *Parental care in mammals.*

Klepzig, K. D., & Taborsky, M. (2011). Costs of delayed dispersal and alloparental care in the fungus-cultivating ambrosia beetle *Xyleborus affinis Eichhoff* (Scolytinae: Curculionidae). *Behavioral Ecology and Sociobiology, 65*(9), 1753-1761 .

Koenig, W. D., & Dickinson, J. L. (2016). *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior.* Cambridge University Press.

Koenig, W. D., & Mumme, R. L. (1996). Levels of analysis and the functional significance of helping behavior. *Readings in Animal Cognition*, 143.

Kokko, H. & Ekman, J. (2002). Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *The American Naturalist*, *160*(4), 468-484.

Kokko, H., Johnstone, R. A., & H., C.-B. T. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 268*(1463), 187-196.

Kokko, H., Johnstone, R. A., & Wright, J. (2002). The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behavioral Ecology, 13*(3), 291-300.

Komdeur, J. (2006). Variation in individual investment strategies among social animals. *Ethology, 112*(8), 729-747.

König, B. (2006). Non-offspring nursing in mammals: general implications from a case study on house mice. In *Cooperation in Primates and Humans* (pp. 191-205). Berlin, Heidelberg: Springer.

Korndeur, J. (1996). Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behavioral Ecology, 7*(3), 326–333.

Kutsukake, N., & Clutton-Brock, T. H. (2006). Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour, 72*(5), 1059-1068.

Langergraber, K. E., Watts, D. P., Vigilant, L., & Mitani, J. C. (2017). Group augmentation, collective action, and territorial boundary patrols by male chimpanzees. *Proceedings of the National Academy of Sciences, 114*(28), 7337-7342.

Lazaro-Perea, C., de Fátima Arruda, M., & Snowdon, C. T. (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour, 67*(4),627-636.

Leclaire, S., Nielsen, J. F., Thavarajah, N. K., Manser, M., & Clutton-Brock, T. H. (2013). Odour-based kin discrimination in the cooperatively breeding meerkat. *Biology Letters, 9*(1), 20121054.

Lehtonen, J., & Jaatinen, K. 2016. Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology, 70*(4), 449-458.

Lessells, C. M. (2002). Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philosophical Transactions of the Royal Society B: Biological Sciences, 357*(1419), 381–403.

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour, 49*(1), 11-20.

Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., . . . Meaney, M. J. (1997). Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. *Science, 277*, 1659-1662.

Lukas, D., Reynolds, V., Boesch, C., & Vigilant, L. (2005). To what extent does living in a group mean living with kin? *Molecular Ecology, 14*(7), 2181-2196.

Macdonald, D. W. (1979). 'Helpers' in fox society. *Nature, 282*, 69–71.

Macdonald, D. W., & Moehlman, P. D. (1982). *Cooperation, Altruism, and Restraint in the Reproduction of Carnivores* (Vol. 5). Perspectives in Ethology.

Madison, D. M. (1984). Group nesting and its ecological and evolutionary significance in overwintering microtus rodents. *Winter Ecology of Small Mammals*, 267-274.

Malcolm, J. R., & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology, 10*(1), 1-13.

Margulis, S. W., Nabong, M., Alaks, G., Walsh, A., & Lacy, R. C. (2005). Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. *Animal Behaviour, 69*(3), 627-634

Marshall, H. H., Sanderson, J. L., Mwanghuya, F., Businge, R., Kyabulima, S., Hares, M. C., . . . Vitikainen, E. I. (2016). Variable ecological conditions promote male helping by changing banded mongoose group composition. *Behavioral Ecology, 27*(4), 978-987.

McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P., & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology, 84*(3), 871-878.

Missakian, E. A. (1974). Mother-offspring grooming relations in rhesus monkeys. *Archives of Sexual Behavior, 3*(2), 135.

Mitani, J. C., & Watts, D. (1997). The evolution of non-maternal caretaking among anthropoid primates: do helpers help? *Behavioral Ecology and Sociobiology, 40*(4), 213-220.

Moehlman, P. D. (1979). Jackal helpers and pup survival. *Nature, 277*, 382–383.

Morris-Drake, A., Christensen, C., Kern, J., & Radford, A. (2019). Experimental field evidence that out-group threats influence within-group behavior. *Behavioral Ecology*.

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359-370.

Moura, A. C. D. A., Nunes, H. G., & Langguth, A. (2010). Food sharing in lion tamarins *(Leontopithecus chrysomelas*): does foraging difficulty affect investment in young by breeders and helpers?. *International Journal of Primatology, 31*(5), 848-862.

Müller, C. A., & Manser, M. B. (2008). Mutual recognition of pups and providers in the cooperatively breeding banded mongoose. *Animal Behaviour*, *75*(5), 1683-1692.

Mullon, C., Reuter, M., & Lehmann, L. (2014). The evolution and consequences of sex-specific reproductive variance. *Genetics, 196*(1), 235-252.

Mumme, R. L. (1992). Do helpers increase reproductive success? *Behavioral Ecology and Sociobiology, 31*(5), 319-328.

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology, 17*(6), 1020-1028.

Murray, M. G., & Gerrard, R. (1984). Conflict in the neighbourhood: Models where close relatives are in direct competition. *Journal of Theoretical Biology, 111*(2), 237-246.

Nelson-Flower, M. J., Hockey, P. A., O'Ryan, C., Raihani, N. J., du Plessis, M. A. & Ridley, A. R. (2011). Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. *Behavioral Ecology*, *22*(3), 559-565.

Nelson-Flower, M. J., Wiley, E. M., Flower, T. P., Ridley, A. R. (2018). Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance. *Journal of Animal Ecology, 87*(5), 1227-1238.

Newton-Fisher, N. (1999). Association by male chimpanzees: a social tactic? *Behaviour, 136*(6), 705–730.

O'Brien, T. G., & Robinson, J. G. (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour, 119*(1-2), 30-50.

O'Donnell, C. F. (2002). Timing of breeding, productivity and survival of long-tailed bats *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae) in cold-temperate rainforest in New Zealand. *Journal of Zoology, 257*(3), 311-323.

Owens, D. D., & Owens, M. J. (1984). Helping behaviour in brown hyenas. *Nature, 308*(5962), 843.

Packer, C., Lewis, S., & Pusey, A. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour, 43*(2), 265-281.

Paul, A. (1999). The socioecology of infant handling in primates: Is the current model convincing? *Primates, 40*(1), 33–46.

Perkeybile, A. M., Delaney-Busch, N., Hartman, S., Grimm, K. J., & Bales, K. L. (2015). Intergenerational transmission of alloparental behavior and oxytocin and vasopressin receptor distribution in the prairie vole. *Frontiers in Behavioral Neuroscience, 9*, 191.

Port, M., Kappeler, P. M., & Johnstone, R. A. (2011). Communal defense of territories and the evolution of sociality. *The American Naturalist, 178*(6), 787-800.

Pusey, A. E., & Packer, C. (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behavioral Ecology, 5*(4), 362–374.

Quenette, P. Y. (1990). Functions of vigilance behaviour in mammals: a review. *Acta Oecologica, 11*(6), 801-818.

Radford, A. N. (2003). Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. *Animal Behaviour, 66*, 1035–1044.

Radford, A. N., Majolo, B., & Aureli, F. (2016). Within-group behavioural consequences of between-group conflict: a prospective review. *Proceedings of the Royal Society, Series B, 283*, 20161567.

Rasa, O. A. (1977). The ethology and sociology of the dwarf mongoose (*Helogale undulata rufula*). *Zeitschrift für Tierpsychologie, 43*(4), 337-406.

Rasa, O. A. (1989). The costs and effectiveness of vigilance behaviour in the dwarf mongoose: implications for fitness and optimal group size. *Ethology Ecology & Evolution, 1*(3), 265-282.

Reeve, H. K. (1992). Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature, 358*(6382), 147.

Reyer, H. U. (1986). Breeder-helper-interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour*, 277-303.

Ridley, A. R., Nelson-Flower, M. J., & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour, 85*(1), 137-142.

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology, 57*(4), 405-435.

Roberts, G., 1996. Why individual vigilance declines as group size increases. *Animal behaviour, 51*(5), 1077-1086.

Roberts, G., & Sherratt, T. N. (1998). Development of cooperative relationships through increasing investment. *Nature, 394*, 175–179.

Roberts, R. L., Williams, J. R., Wang, A. K., & Carter, C. S. (1998). Cooperative breeding and monogamy in prairie voles: influence of the sire and geographical variation. *Animal Behaviour, 55*(5), 1131-1140.

Robinson, J. G., & O'Brien, T. G. (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour, 119*(1-2), 30-50.

Rood, J. P. (1978). Dwarf Mongoose Helpers at the Den. *Zeitschrift für Tierpsychologie, 48*(3), 277-287.

Rood, J. P. (1980). Mating relationships and breeding suppression in the dwarf mongoose. *Animal Behaviour, 28*(1), 143-150.

Rood, J. P. (1983). The social system of the dwarf mongoose. *Advances in the Study of Mammalian Behaviour*, 25–88.

Rood, J. P. (1987). Dispersal and intergroup transfer in the dwarf mongoose. In *Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics*, 85-103.

Rood, J. P. (1990). Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour, 39*(3), 566-572.

Russell, A. F., Young, A. J., Spong, G., Jordan, N. R., & Clutton-Brock, T. H. (2006). Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society B: Biological Sciences, 274*(1609), 513-520.

Russell, Y. I., & Phelps, S. (2013). How do you measure pleasure? A discussion about intrinsic costs and benefits in primate allogrooming. *Biology and Philosophy, 28*(6), 1005-1020.

Rutherford, M. C., Mucina, L., & Powrie, L. W. (2006). Biomes and bioregions of southern Africa. *The vegetation of South Africa, Lesotho and Swaziland, 19*, 30-51.

Rymer, T. L., & Pillay, N. (2014). Alloparental care in the African striped mouse *Rhabdomys pumilio* is age-dependent and influences the development of paternal care. *Ethology, 120*(1), 11-20.

Rymer, T., Pillay, N., & Schradin, C. (2013). Extinction or survival? Behavioral flexibility in response to environmental change in the African striped mouse *Rhabdomys*. *Sustainability, 5*(1), 163-186.

Sachs, J., Mueller, U., Wilcox, T., & Bull, J. (2004). The evolution of cooperation. *The Quarterly Review of Biology, 79*(2), 135-160.

Sánchez, S., Peláez, F., Gil-Bürmann, C., & Kaumanns, W. (1999). Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology: Official Journal of the American Society of Primatologists, 48*(2), 99-111.

Schaffner, C. M., & French, J. A. (1997). Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate. *Animal Behaviour, 54*(1), 171-180.

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour, 62*(2), 265-271.

Schradin, C., Lindholm, A. K., Johannesen, J. E., Schoepf, I., Yuen, C.-H., Koenig, B., & Pillay, N. (2012). Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology, 21*(3), 541-553.

Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature, 308*, 541–543.

Sharpe, L. L. (2005). Play does not enhance social cohesion in a cooperative mammal. *Animal Behaviour, 70*(3), 551–558.

Sherman, P. W., Lacey, E. A., Reeve, H. K., & Keller, L. (1995). Forum: The eusociality continuum. *Behavioral Ecology, 6*(1), 102-108.

Shields, W. M. (1984). Barn swallow mobbing: self-defence, collateral kin defence, group defence, or parental care? *Animal Behaviour, 32*(1), 132-148.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1480), 539-559.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*(5648), 1231-1234.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3099-3104

Smith, T. G., Siniff, D. B., Reichle, R. & Stone, S. (1981). Coordinated behavior of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. *Canadian Journal of Zoology*, *59*(6), 1185-1189.

Snyder-Mackler, N., Alberts, S. C., & Bergman, T. J. (2012). Concessions of an alpha male? Cooperative defence and shared reproduction in multi-male primate groups. *Proceedings of the Royal Society B: Biological Sciences, 279*(1743), 3788.

Solomon, N., & French, J. (1997). *Cooperative Breeding in Mammals.* New York: Cambridge University Press.

Song, Z., Tai, F., Yu, C., Wu, R., Zhang, X., Broders, H., He, F. & Guo, R. (2010). Sexual or paternal experiences alter alloparental behaviour and the central expression of ERα and OT in male mandarin voles (*Microtus mandarinus*). *Behavioural Brain Research, 214*(2), 290-300.

Sparkman, A. M., Adams, J. R., Steury, T. D., Waits, L. P., & Murray, D. L. (2010). Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). *Behavioral Ecology, 22*(1), 199-205.

Spruijt, B. M., Hooff, J. A., & Gispen, W. H. (1992). Ethology and neurobiology of grooming behavior. *Physiological Reviews, 72*, 825-852.

Stacey, P., & Koenig, W. (1990). *Cooperative breeding in birds: long term studies of ecology and behaviour*. Cambridge University Press.

Stacey, P. B. & Ligon, J. D. (1987). Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *The American Naturalist, 130*(5), 654-676.

Taborsky, M. & Limberger, D. (1981). Helpers in fish. *Behavioral Ecology and Sociobiology*, *8*(2), 143-145

Thompson, F. J., Marshall, H. H., & Cant, M. A. (2019). Live long and prosper: durable benefits of early-life care in banded mongooses. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *374*(1770).

Thorley, J., Mendonça, R., Vullioud, P., Torrents-Ticó, M., Zöttl, M., Gaynor, D. & Clutton-Brock, T., (2018). No task specialization among helpers in Damaraland mole-rats. *Animal Behaviour*, 143(1), 9-24

Thornton, A., & McAuliffe, K. (2006). Teaching in Wild Meerkats. *Science, 313*(5784), 227-229.

Thünken, T., Eigster, M., & Frommen, J. G. (2014). Context-dependent group size preferences in large shoals of three-spined sticklebacks. *Animal Behaivour, 90*, 205-210.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology, 46*(1).

Vitikainen, E. I., Marshall, H. H., Thompson, F. J., Sanderson, J. L., Bell, M. B., Gilchrist, J. S., . . . Cant, M. A. (2017). Biased escorts: offspring sex, not relatedness explains alloparental care patterns in a cooperative breeder. *Proceedings of the Royal Society B: Biological Sciences, 284*(1854), 20162384.

Vitikainen, E. I., Thompson, F. J., Marshall, H. H., & Cant, M. A. (2019). Live long and prosper: durable benefits of early-life care in banded mongooses. *Philosophical Transactions of the Royal Society B, 374*(1770), 20180114.

Waal, F. B. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution, 18*(5), 433-459.

Waterman, J. M., & Roth, J. D. (2008). The influence of sex and sociality on parasite loads in an African ground squirrel. *Behavioral Ecology, 19*(5), 1006-1011.

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology, 38*(4), 237-244.

Whitehead, H., Antunes, R., Gero, S., Wong, S. N., Engelhaupt, D., & Rendell, L. (2012). Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *International Journal of Primatology, 33*(5), 1142-1164.

Wich, S., & Sterck, E. (2007). Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. *Behaviour, 144*(12), 1583-1598.

Wiley, R. H., & Rabenold, K. N. (1984). The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution* , 609-621.

Wilkinson, G. (1992). Communal nursing in the evening bat, *Nycticeius humeralis*. *Behavioural Ecology and Sociobiology, 31*, 225-235.

Wisenden, B. D. (1999). Alloparental care in fishes. *Reviews in Fish Biology and Fisheries, 9*(1), 45-70.

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M. & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior, 54*(1), 170-177.

Woodroffe, R., & Macdonald, D. W. (2000). Helpers provide no detectable benefits in the European badger (*Meles meles*). *Journal of Zoology, 250*, 113-119.

Woodroffe, R., & Vincent, A. (1994). Mother's little helpers: Patterns of male care in mammals. *Trends in Ecology and Evolution, 9*(8), 294-297.

Wright, J. (1997). Helping-at-the-nest in Arabian babblers: signalling social status or sensible investment in chicks? *Animal Behaviour, 54*(6), 1439-1448.

Wright, J. (1999). Altruism as a signal: Zahavi's alternative to kin selection and reciprocity. *Journal of Avian Biology, 30*(1), 108-115.

Wright, J., Berg, E., Kort, S. R., Khazind, V., & Maklakov, A. A. (2001). Cooperative sentinel behaviour in the Arabian babbler. *Animal Behaviour, 62*(5), 973-979.

Zahavi, A. (1990). Arabian babblers: the quest for social status in a cooperative breeder. *Cooperative Breeding in Birds*, 103-130.

Zahavi, A. (1995). Altruism as a handicap: the limitations of kin selection and reciprocity. *Journal of Avian Biology, 26*(1), 1-3.

Zahed, S. R., Kurian, A. V., & Snowdon, C. T. (2010). Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 72*(4), 296-306.

Zöttl, M., Vullioud, P., Goddard, K., Torrents-Ticó, M., Gaynor, D., Bennett, N. C., & Clutton-Brock, T. (2018). Allo-parental care in Damaraland mole-rats is female biased and age dependent, though independent of testosterone levels. *Physiology & Behavior, 193*, 149-153.